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Fishery Bulletin

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Awards

U.S. Department of Commerce
Seattle, Washington

The Publications Advisory Committee of the National Marine Fisheries Service has announced the best publications authored by NMFS scientists and published in the *Fishery Bulletin* for 1987 and 1988 and *Marine Fisheries Review* for 1986 and 1987. Only effective and interpretive articles which significantly contribute to the understanding and knowledge of NMFS mission-related studies are eligible, and the following pages were judged as the best in meeting this requirement.

Fishery Bulletin 1987

Dean W. Ahrenholz, Walter R. Nelson, and Sheryan P. Epperly
Population and fishery characteristics of Atlantic menhaden, *Brevoortia tyrannus*. Fishery Bulletin, U.S. 85:569-600. Dean Ahrenholz and Sheryan Epperly are with the Beaufort Laboratory, Southeast Fisheries Science Center, Beaufort, North Carolina; Walter Nelson is with the Pascagoula Laboratory, Southeast Fisheries Science Center, Pascagoula, Mississippi.

Fishery Bulletin 1988

Edmund S. Hobson and James R. Chess
Trophic relations of the blue rockfish, *Sebastes mystinus*, in a coastal upwelling system off northern California. Fishery Bulletin, U.S. 86:715-743. Both authors are with the Tiburon Laboratory, Southwest Fisheries Science Center, Tiburon, California.

Marine Fisheries Review 1986

Austin B. Williams
Lobsters—Identification, world distribution, and U.S. trade. Marine Fisheries Review 48(2):1-36. The author is with the NMFS Systematics Laboratory, National Museum of Natural History, Washington, D.C.

Marine Fisheries Review 1987

Arthur W. Kendall Jr., and Ann C. Matarese
Biology of eggs, larvae, and epipelagic juveniles of sablefish, *Anoplopoma fimbria*, in relation to their potential use in management. *Marine Fisheries Review* 49(1):1-13. Both authors are with the Resource Assessment & Conservation Engineering Division, Alaska Fisheries Science Center, Seattle, Washington.

John Alan Gulland
1926–1990

We report with sadness the death of John Gulland on June 24, 1990 after a long illness. He is remembered for his work on population dynamics and effects of exploitation on fish stocks, and for his clear insights into the problems of conservation and effective management of fisheries resources.

John Gulland trained at Cambridge as an applied mathematician. Early in his career, he joined the Fisheries Laboratory at Lowestaft. At this time, fisheries in the North Atlantic were rebounding after the hiatus of World War II and it had become clear that scientific management was required. Various international commissions were established for fisheries management, each of which had a scientific committee associated with it. It was not long before Gulland began to play a major role in these committees, insisting on obtaining from each participating country the data needed from their fisheries. It was his careful analysis of these fisheries data and his scientific conclusions that cut through the hypocrisy that was often a mask for political considerations.

In the early sixties, Gulland was loaned to Australia, which in turn loaned him to the Committee of Three, established by the International Whaling Commission (IWC) in 1960 to carry out a scientific assessment of the whale stocks. Gulland quickly became such a valuable member of the group that it was expanded to the Committee of Four. After the Committee made its report, and suggested a substantial cutback in whale quotas, the Food and Agriculture Organization (FAO) of the United Nations was given the task of continuing the studies on status of whale stocks. About this time Gulland transferred to FAO and continued this activity with the IWC for several years.

Also in his new post at FAO, Gulland began to work on the fisheries problems of developing countries around the world. He brought to these problems the same logical mind

and disdain for political solutions that he had earlier shown in his dealings with North Atlantic fisheries. His experience in FAO and a developing association with the College of Fisheries at the University of Washington led him to write several books. These include: *The Fish Resources of the Ocean* (1972), *The Management of Marine Fisheries* (1974, 1977), and *Fish Stock Management* (1977).

Gulland's many accomplishments have been recognized in many ways. He was named Keynote Speaker at the annual meeting of the American Fisheries Society (1977), and, more importantly, he was elected to the Royal Society (1984). He retired from FAO in 1984 and returned to England where he became associated with Imperial College, London. He continued to work on a variety of marine resource problems, as he was doing at the time of his death on 24 June 1990.

While Gulland was an outstanding scientist who developed much of fisheries science and management techniques that are valid today, he was not above "back-of-the-envelope" calculations. He would often use these to demolish opponents who were using apparently sophisticated analyses to obfuscate rather than to clarify. But he also had a delightful lighthearted side to his character. An incident that reflects this side of his personality occurred while he served as an adviser to the Commission for the Conservation of Antarctic Living Marine Resources. The group arranged for him to visit the South Pole in January 1985. While there, he took part in a cricket match on the Beardmore Glacier (the largest glacier in the world). There was no doubt that this was the most southerly cricket match ever played, and as such he often stated that this was the capstone of his career.

Douglas G. Chapman

Erratum

Sturm, Maxwell G. de L., and Premila Salter
Age, growth, and reproduction of the king mackerel *Scomberomorus cavalla* (Cuvier) in Trinidad waters. Fish. Bull., U.S. 88:361–370.

The Abstract, p. 361, should be corrected as follows:

In the fourth sentence, L_∞ should be replaced by L_t in both von Bertalanffy equations, and the male t_0 value should read 1.79 rather than 1.80.

In the fifth sentence, "...peak spawning from October through March..." should read "September through March..."

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Trophic Relations of Juvenile Pacific Salmon off the Oregon and Washington Coast

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Abstract. – Feeding habits of juvenile coho *Oncorhynchus kisutch*, chinook *O. tshawytscha*, chum *O. keta*, and sockeye *O. nerka* salmon were examined from collections taken off the Oregon–Washington coast during the summers of 1980–85. The major prey of both coho and chinook salmon juveniles were larval and juvenile fishes, although a substantial proportion of the diet of coho salmon consisted of invertebrates such as euphausiids, decapod larvae, and hyperiid amphipods. Juvenile chum and sockeye salmon had a more varied diet consisting generally of smaller prey, such as juvenile euphausiids, copepods, amphipods, and chaetognaths. Diet overlap was highest between coho and chinook salmon. Both dietary overlap and diversity varied substantially among cruises and individual collections.

Pronounced seasonal and interannual variations occurred in the utilization of the major prey taxa by coho and chinook salmon which may have been related to highly variable oceanographic conditions prevailing during this period. Areal (latitudinal and cross-shelf) variations were of lesser importance in the diets of juvenile coho and chinook salmon.

Manuscript accepted 29 May 1990.
Fishery Bulletin, U.S. 88:617–636.

Until recently, much of the interannual variability in the survival of Pacific salmon *Oncorhynchus* spp. was believed to be a result of conditions occurring in freshwater. It was surmised that by releasing high and relatively constant numbers of hatchery smolts in freshwater, much of the interannual variation in salmon production could be circumvented. Contrary to this assumption, a number of recent studies have found that a substantial portion of the total natural mortality for most salmon species may occur during estuarine and early marine residence (Parker 1968, 1971; Mathews and Buckley 1976; Bax 1983; Furnell and Brett 1986; Fisher and Pearcy 1988). For coho salmon *O. kisutch* originating from Oregon and Washington rivers, peak mortality appears to happen very early in the ocean, perhaps within the first month, and year-class size appears to be well established by the end of the first summer in the ocean (Pearcy 1988).

We still do not know the exact cause of this early ocean mortality. Annual variability in ocean survival of Oregon–Washington salmon stocks appears to be quite large. Both depensatory environmental factors, such as upwelling (Gunsolus 1978, Nickelson 1986), and compensatory biotic interactions such as competition or predation (Peterman 1982, Peterman and Routledge 1983, McGie 1984) have been implicated in the early ocean mortality of juvenile salmon. In either situation, early ocean feeding may be important, and perhaps critical, to growth and survival of salmonids.

Knowledge of the feeding habits and diet variability of juvenile salmon in the coastal ecosystem off Washington and Oregon is incomplete. Peterson et al. (1982) described the diets of juvenile coho, chinook *O. tshawytscha*, and chum *O. keta* salmon for one month (June 1979) and three different geographical areas off southern Washington and Oregon. Emmett et al. (1986) examined seasonal variations in juvenile coho and chinook salmon feeding habits from three time-periods during 1980, but did not examine geographic variations in any detail. There were substantial within and between-study differences in the food composition of these salmonids, although the relative importance of the geographical and temporal components of the variability could not be assessed because of the different sampling designs of the two studies.

This paper describes the diet composition and feeding relationships of juvenile coho, chinook, chum, and sockeye (*O. nerka*) salmon collected from coastal waters off Washington and Oregon during a series of summer purse-seine collections made from 1980 to 1985. Oceanographic conditions and biological productivity were highly variable during this period, both seasonally and interannually (Fisher and Pearcy 1985, Brodeur and Pearcy 1986), and thus provided a fortuitous situation in which to examine the effects of environmental variability on juvenile salmon feeding habits. In addition to examining the interannual variation in feeding, the broad seasonal and geographic coverage of the sampling permitted more detailed intra-annual and areal resolution than was previously possible. Particular detail will be provided for coho and chinook salmon juveniles, which were the dominant salmonids caught (Pearcy 1984, Pearcy and Fisher In press). Although the importance of other potential sources of variability in the diet, such as those attributable to the time of day and predator size, is recognized, these additional factors are discussed in detail elsewhere (Brodeur and Pearcy 1987, Brodeur In press).

Methods

Collection of stomachs

Juvenile salmon were collected with small-mesh (32 mm stretched), large volume (up to 1 million m^3) herring purse seines (Pearcy and Fisher 1988). Sampling was conducted in known areas of salmon concentration in 1980; in following years, predesignated stations were sampled along parallel transect lines spaced approximately 37 km apart (Fig. 1). Along each transect, stations were located every 9.3 km (5 miles) beginning onshore at the 37-m (20 fm) isobath and continuing out to 56 km from the coast or until no juvenile salmon were caught. Data from a total of 15 cruises have been included in this study, with at least one cruise taking place during every month from May through September (Table 1). June was the most intensely sampled month and was sampled during each of the 6 years of the study.

Most collections were made during daylight or twilight, although several complete diel series were made (Brodeur and Pearcy 1987). Circular, quantitative haul sets were made at most stations, although a small proportion of the fish used in this study were collected from sets which were held open for up to 45 minutes or from non-quantitative sets (Pearcy and Fisher 1988). After pursing the net, the catch was then concentrated in the bunt of the seine, and either dip-netted out from the seine or hauled onboard the stern of the sampling vessel. Total sampling time for most sets was approximately 20 minutes. Ancillary physical (temperature and salinity) and biological (chlorophyll *a* and some zooplankton) data were collected before or after the fish collections. A detailed listing of the station locations and many of the physical and biological measurements are given by Fisher and Pearcy (1985) and Brodeur and Pearcy (1986).

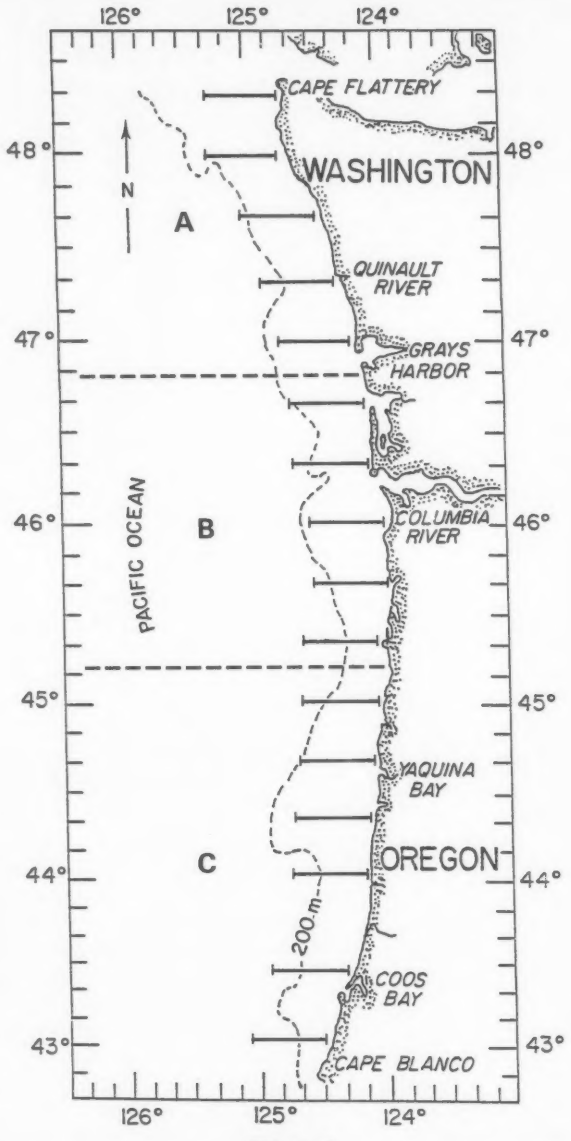

Figure 1
Location of sampling transects and geographic subareas defined in this study.

Table 1
Summary of sampling off Oregon and Washington by cruise from 1980 to 1985. Number of sets includes only quantitative, round hauls taken within 56 km of the coast.

Cruise no.	Year	Dates of cruise	Latitudinal range sampled (North latitude)	Number of sets
1	1980	June 20–28	46°20′–44°30′	33
2	1981	May 16–25	46°35′–44°30′	63
3	1981	June 9–19	46°35′–43°11′	67
4	1981	July 9–19	46°35′–44°25′	71
5	1981	August 8–19	46°35′–43°11′	66
6	1982	May 19–June 2	48°20′–44°00′	62
7	1982	June 7–22	47°20′–44°20′	56
8	1982	Sept. 4–14	47°20′–44°20′	40
9	1983	May 16–27	48°20′–44°20′	57
10	1983	June 9–27	48°20′–43°00′	58
11	1983	Sept. 15–24	48°20′–43°28′	52
12	1984	June 6–20	48°20′–43°28′	66
13	1984	July 19–30	48°00′–44°00′	40
14	1984	Sept. 1–15	48°20′–44°00′	63
15	1985	June 10–25	48°00′–43°27′	78
			Total	865

Once aboard, the juvenile salmon were quickly separated from the rest of the catch and anaesthetized in MS-222 to prevent regurgitation during handling. Each fish was tentatively identified, measured to the nearest mm (fork length), individually labeled, and either preserved whole in formalin after slitting the body cavity (1980 and part of 1981) or frozen whole in a −20°C freezer.

In the laboratory ashore, species identifications were verified and individual wet weights were recorded to the nearest 0.1 g. Stomachs were then removed from a random subsample of up to 10 individuals per species for each collection, with the stipulation that the entire size range of each species represented in the sample be included. Stomachs were individually preserved in a 10% formalin solution and then transferred to a 70% ethanol solution prior to examination. Subyearling and yearling juveniles of each species in their first year in the ocean were distinguished from adult fish using scale analysis (Fisher and Pearcy 1988).

Stomach analysis

Stomachs were opened and the relative fullness was subjectively assessed on a scale from 0 (empty) to 5 (fully distended). The entire stomach contents were blotted on absorbent paper to remove excess moisture and weighed to the nearest 1 mg. The contents were identified under a dissecting microscope to the lowest possible taxonomic level and life-history stage. During this analysis, each prey taxon was assigned a digestion code ranging from 0 (well digested) to 4 (fresh), and a digestion level for the entire stomach was derived from these codes based on the relative proportion by weight of each taxon. Each prey taxon was then enumerated, blotted to remove excess moisture, and weighed to the nearest 1 mg.

Statistical analyses

Three measures were used to determine the importance of each prey taxon to a particular predator: the percent frequency of occurrence in non-empty stomachs (F), the percent of total number of prey organisms (N), and the percent of total weight of prey organisms (W). These measures were combined into a single number, the Index of Relative Importance (IRI = F (N + W)), modified from that described by Pinkas et al. (1971) using weight instead of volume, so that comparisons can easily be made between the relative prey composition of different collections or species. Prey items that were digested or taxa difficult to count, such as gelatinous organisms, were not assigned IRI values. The IRI values were then converted to percent of total IRI for each predator species.

Niche breadth, expressed as the scope of utilization of food resources by each predator species, was calculated using the Shannon-Weaver formula:

$$H'_i = -\sum_{j=1}^{n} P_{ij} (\log_2 P_{ij})$$

where P_{ij} = the proportion by weight of a prey item j in predator i (Petraitis 1979). This index is influenced by both the number of species in the stomachs and the evenness with which they are distributed among the stomachs, and attains a maximum value (H'_{max}) of $\log_2$ (number of prey taxa). The ratio of H′ to H'_{max} provides a measure of the evenness with which the resources are distributed among the predators (Pielou 1977).

Diet overlap was calculated among all species for the entire data set and between coho and chinook by cruise or collection where at least 10 stomachs of each species were examined. Schoener's Percent Similarity Index (PSI) was used since it was found to have the most favorable properties within the range of normal overlap values in the absence of prey availability data (Linton et al. 1981, Wallace 1981) where:

$$PSI = [1.0 - 0.5 (\sum | P_{ij} - P_{hj} |)] \times 100$$

where P_{ij} is the proportion by weight of food category

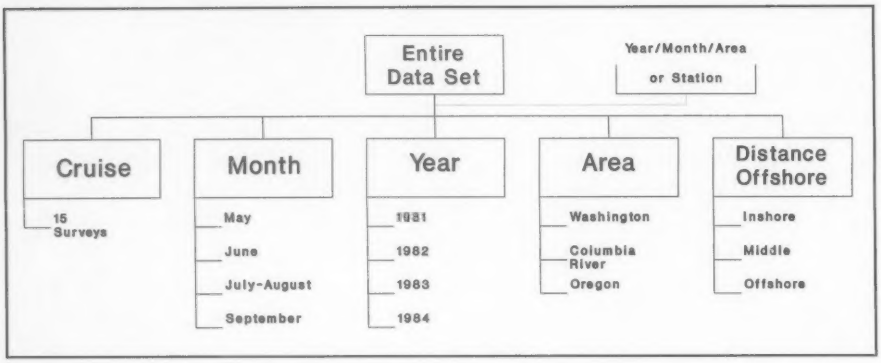

Figure 2
Hierarchy of data groupings used in the analysis of dietary variations in juvenile Pacific salmon.

j in the diet of species i, and P_{hj} is the proportion by weight of food category j in the diet of species h. This index ranges from 0 when two predators have no prey in common to 100 when they have identical diets. Overlap values greater than 60 are generally considered significant. Food availability was considered to be the same for all predators in any one comparison.

The detailed stomach data were then truncated to major taxonomic categories so that general trends in feeding by month, year, and area could be elucidated. Stomach samples of each salmon species were grouped into smaller subsets in a number of different ways to examine diet variability (Fig. 2). The diets of coho and chinook salmon were first examined by cruise so that temporal variability between cruises could be assessed. Data were then grouped by month into four time-periods: May (three cruises), June (six cruises), July–August (three cruises), and September (three cruises). Seasonal changes in diets were then analyzed for these time-periods, regardless of the year or area of collection. Similarly, diets were analyzed by year of collection for those years (1981–84) when multiple cruises exist. North-south geographic variations were examined for each of three subareas within the total sampling area. The collections were stratified latitudinally (Fig. 1) into three areas: (A) north of 46°40′N, (B) between 46°40′N and 45°20′N, and (C) south of 45°20′N (Brodeur et al. 1987a). Food habits were examined for each of these areas for all months and years combined. Finally, diets were examined within each year/month/area subset or by collection so that smaller-scale variations in the food and dietary overlap could be assessed.

Another potential source of geographic variability was that associated with inshore-offshore variations in prey availability and abundance. This source of variation was examined for several cruises where a large number of collections of coho or chinook salmon were obtained far offshore. For these cruises, collections were divided into inner shelf (<18 km from shore), middle shelf (18–37 km), and outer shelf (>37 km) stations. Diets of chum and sockeye salmon were also examined for variation with respect to the different factors when sample sizes were adequate.

The relative importance of the interannual, seasonal, and geographic variations seen in the diets of coho and chinook juveniles was tested by comparing the presence and absence of a particular major prey category using a variance test of binominally distributed data (Snedecor and Cochran 1967) for each factor individually irrespective of the others. When a value exceeded the tabulated 0.05 chi-square percentage, the null hypothesis that the diets were similar was rejected.

Results

Coho salmon

General food habits Juvenile coho salmon had a relatively diverse diet with many different prey categories represented in the stomachs examined for all years combined (Appendix Table 1). A high percentage (95.2%) of the stomachs contained food, and the overall stomach fullness ($\bar{x}$ 3.0) and digestion ($\bar{x}$ 2.3) codes were high indicating that many of the juvenile coho had fed prior to capture.

The primary food groups consumed by juvenile coho salmon were fishes, decapod larvae, amphipods, euphausiids, pteropods, and copepods (Appendix Table 1). Larval and juvenile fishes were the most important prey making up 72% of the total weight and 60% of the total IRI. Rockfishes *Sebastes* spp., northern anchovies *Engraulis mordax*, and Pacific sand lance *Ammodytes hexapterus* were the dominant fish taxa. Although other fish families were represented in the diet, notably the Osmeridae, Cottidae, Hexagrammidae, and Pleuronectidae, each of these families made up less than 1% of the total diet by percent IRI.

Table 2
Food habits by percent weight of major food categories for coho salmon, by cruise, off Oregon and Washington.

	1980	1981				1982			1983			1984			1985
	June	May	June	July	Aug.	May	June	Sept.	May	June	Sept.	June	July	Sept.	June
Prey category															
Fishes	82.8	75.6	73.3	17.6	65.1	75.6	75.6	83.1	73.2	82.7	81.9	83.6	26.1	61.0	82.1
Euphausiids	4.4	2.0	11.0	22.2	31.7	16.0	13.3	2.9	7.3	0.7	10.5	4.9	15.2	17.5	6.3
Decapods	3.5	8.4	11.9	3.5	0.3	6.9	4.2	0.6	12.8	15.6	0.1	10.9	13.2	5.6	6.3
Hyperiids	0.9	0.7	0.4	3.9	1.2	0.8	3.9	5.7	1.5	0.6	3.9	0.1	3.5	13.4	4.8
Pteropods	0.2	10.1	1.6	51.1	0.3	0.3	0.3	6.7	1.6	<0.1	2.1	—	0.1	0.5	<0.1
Copepods	<0.1	0.2	0.3	0.3	0.1	<0.1	<0.1	<0.1	1.3	0.1	<0.1	0.3	0.4	<0.1	<0.1
Insects	<0.1	—	<0.1	0.1	0.1	0.2	0.1	<0.1	0.3	<0.1	<0.1	<0.1	40.0	<0.1	0.1
Cephalopods	6.9	0.6	0.3	—	1.2	—	—	0.9	<0.1	—	1.3	—	0.4	1.0	—
Other*	1.1	0.4	0.8	0.8	<0.1	1.8	1.0	<0.1	0.2	<0.1	0.1	0.1	1.2	<0.1	0.4
Predator characteristics															
No. stomachs	77	245	139	115	94	57	124	144	112	125	102	81	75	61	101
No. empty	1	15	13	3	6	1	4	5	1	7	3	7	7	3	3
Mean length	167.9	153.3	173.7	200.4	231.6	151.9	149.6	247.4	164.7	191.5	270.5	175.7	208.9	275.0	188.4
Length range	81–292	111–238	113–314	92–390	138–386	124–188	120–220	137–410	117–421	125–349	152–420	121–247	144–347	177–366	113–262
Mean no. prey	17.8	26.9	45.3	123.2	38.1	9.1	12.1	97.3	35.8	37.2	61.5	20.7	35.3	80.7	35.3
Mean wt. prey	1.46	0.57	1.15	1.40	2.28	0.59	0.50	2.85	0.91	1.23	5.35	1.16	0.70	0.88	1.54

*Includes polychaetes, chaetognaths, gammarids, isopods, cumaceans, cirripedes, mysids, and gelatinous zooplankton.

Many invertebrate prey also occurred frequently or were important numerically in the diet of juvenile coho salmon, but were much less important than fish by weight (Appendix Table 1). Principal invertebrate prey were *Cancer* crab megalopae, the hyperiid amphipods *Hyperoche medusarum* and *Themisto pacifica*, the euphausiids *Thysanoessa spinifera* and *Euphausia pacifica*, and the pteropod *Limacina helicina*. Numerous other species of decapod larvae and amphipods were eaten, as well as copepods and insects, but were of lesser importance. Juvenile *Loligo* squid were also important prey by weight.

Temporal variations Some between-cruise variability in the weight composition of the major food categories was evident (Table 2). During June 1980, coho salmon consumed mainly fishes, although cephalopods were relatively important compared with other cruises. Except during July, fishes dominated the diet during 1981. Pteropods, mainly *L. helicina*, comprised over one-half the total weight of prey in July 1981. Fishes (mostly *A. hexapterus* and *E. mordax*) and euphausiids (mainly *T. spinifera*) dominated the diet during 1982. During 1983 and 1984, coho salmon juveniles fed more upon decapod larvae than during most other years (Table 2). Several anomalous prey items of more southerly origin appeared in the diet in 1983 and 1984, including the euphausiid *Nyctiphanes simplex*, the pteropod *Euclio pyrimidata*, and the hyperiid amphipod *Vibilia* spp. The greatest number of major prey categories were found during July 1984 when terrestrial insects made up over a third of the biomass found in the coho salmon stomachs. One large lepidopteran, *Choristoneura occidentalis*, comprised greater than 37% of the total prey IRI. The diet during June 1985 resembled that of June 1982 at both the specific and general taxonomic levels.

Based on the percent of IRI for the major prey categories, juvenile coho salmon diets changed somewhat as the summer progressed (Fig. 3). Fishes were the main prey during May, although decapod larvae and pteropods were important numerically. During June, fishes and decapod larvae were the primary prey, with amphipods and euphausiids of relatively minor importance. By July and August, fish consumption decreased substantially, and pteropods and euphausiids were the major taxa consumed. Fishes were again the dominant food in September, but their importance was based mainly on weight because individual fish in the stomachs were comparatively larger. In September, pteropods, euphausiids, and amphipods were important prey numerically.

Geographic variations Diets of juvenile coho salmon in the three geographic areas were similar in that the same major prey categories were represented, despite differences in mean size of salmon among the regions. Fishes, decapod larvae, euphausiids, pteropods, and

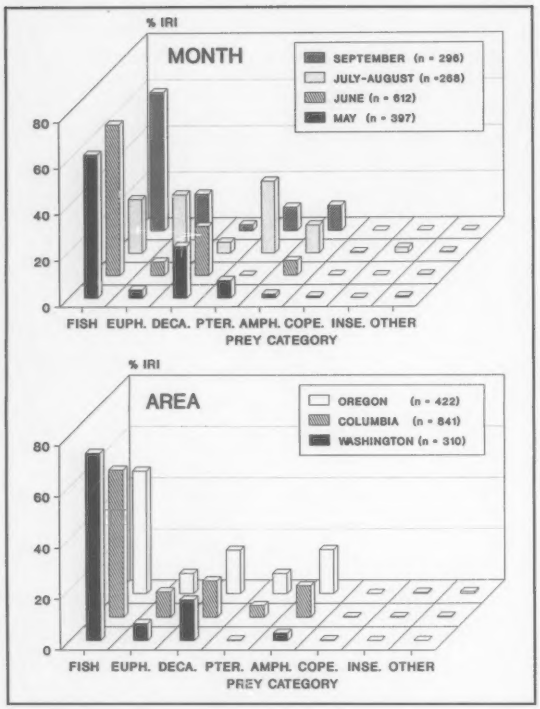

Figure 3

Juvenile coho salmon diets by month and area for the major prey categories as a percent of total IRI. Sample sizes (no. of fish with food) for each subset are given in the legend. All figures include data collected off Washington and Oregon, 1980–85.

amphipods were the dominant prey in each area based on IRI proportions (Fig. 3). The relative proportions of the major prey categories were similar among the regions, although fishes were more important off Washington.

Few differences were observed among the three regions even at the lowest taxonomic levels. *Engraulis mordax* and *Sebastes* spp. were the dominant fish prey by weight in all three regions. The Washington area differed somewhat from the other regions in that *Cancer* larvae were the dominant invertebrate taxa numerically, whereas *L. helicina*, *T. spinifera*, and *H. medusarum* were dominant in the other regions.

Chinook salmon

General food habits Fishes dominated the diet of juvenile chinook salmon, occurring in over 85% of the stomachs that contained food ($n = 795$), and accounting for almost 87% of the total IRI for all years combined (Appendix Table 1). The overall mean stomach fullness (2.8) and digestion (2.3) states were similar to that of coho. Also resembling the diet of coho salmon, the main fish prey identified were *E. mordax*, *Sebastes* spp., and *A. hexapterus*, but cottid juveniles (*Hemilepidotus spinosus*) were also frequently eaten. Pleuronectid and agonid larvae were more common in the diets of juvenile chinook salmon.

Many invertebrate species were also represented in juvenile chinook salmon diets. The relative importance of the various invertebrate taxa was similar to that found for coho salmon. Decapod larvae, euphausiids, and hyperiid amphipods were the dominant invertebrate groups consumed. The dominant species in these prey categories were *C. oregonensis* megalopae, *T. spinifera*, and *H. medusarum*, respectively (Appendix Table 1). Copepods and mysids were generally more important, and pteropods and insects less important, in comparison with juvenile coho salmon.

Temporal variations Between-cruise variability in the consumption of the major prey taxa was less pronounced for chinook salmon than for coho salmon (Table 3). Fishes comprised 75% or more of the biomass consumed during every cruise, with the exception of July 1981 when euphausiids and pteropods were also major prey. The only other invertebrate taxa to contribute substantially in other cruises were cephalopods (May and June 1981), euphausiids (May 1982 and July 1984) and decapod larvae (May and June 1983). In contrast to the diet of coho salmon, insects were unimportant during July 1984 (Table 3).

Seasonally, the relative IRI proportions of fishes, decapod larvae, and euphausiids were similar for chinook salmon (Fig. 4). The diets contained more major prey categories during July–August when small zooplankton prey (copepods, pteropods, decapod larvae, and hyperiid amphipods) were important numerically. This may be due to the smaller mean size of chinook salmon collected this period; in July–August, there was an influx of subyearling chinook salmon into the sampling area. Fishes were again the dominant prey in September, although hyperiid amphipods remained important numerically.

Geographic variations The feeding patterns of juvenile chinook salmon were fairly consistent by major taxonomic categories among the three regions (Fig. 4). Fishes were the major prey by frequency of occurrence and weight in all three geographic areas, although the dominant species varied somewhat. Off Washington, *A. hexapterus*, *Sebastes* spp., and *H. spinosus* were the main fish prey consumed. *Engraulis mordax* and *H. spinosus* were the dominant prey in the Columbia region, whereas *E. mordax* dominated the diet off Oregon (>65% of the total IRI).

Table 3
Food habits by percent weight of major food categories for chinook salmon, by cruise, off Oregon and Washington.

	1980	1981				1982			1983			1984			1985
	June	May	June	July	Aug.	May	June	Sept.	May	June	Sept.	June	July	Sept.	June
Prey category															
Fishes	92.7	84.5	75.4	38.6	97.3	81.9	94.7	91.9	89.0	80.4	98.2	89.5	75.0	88.5	87.8
Euphausiids	0.1	4.1	0.3	32.7	0.6	13.2	0.4	0.6	1.1	0.1	<0.1	0.1	10.0	6.8	6.3
Decapods	0.4	2.8	8.8	6.9	0.3	3.9	3.1	<0.1	9.4	13.8	0.4	5.2	6.2	2.3	4.9
Hyperiids	—	<0.1	<0.1	3.3	0.5	0.6	<0.1	3.6	<0.1	0.4	0.5	0.2	2.5	1.5	0.3
Pteropods	—	0.1	<0.1	10.6	0.4	0.1	<0.1	—	0.1	<0.1	—	—	—	<0.1	—
Copepods	0.4	<0.1	<0.1	0.4	0.5	<0.1	<0.1	—	<0.1	0.6	<0.1	2.9	5.8	—	<0.1
Insects	—	<0.1	0.8	0.2	<0.1	—	—	0.6	—	—	<0.1	—	—	0.6	<0.1
Cephalopods	—	7.7	14.1	—	—	0.9	—	3.1	0.1	3.6	0.4	1.2	—	0.1	0.3
Other*	6.2	—	0.2	6.9	0.3	<0.1	<0.1	—	<0.1	—	0.5	0.2	0.6	0.1	0.5
Predator characteristics															
No. stomachs	14	63	32	53	32	121	112	10	95	27	89	60	21	37	74
No. empty	0	7	2	6	2	5	2	0	3	2	1	11	2	3	3
Mean length	232.5	181.8	196.5	152.9	165.0	218.9	203.7	322.9	192.6	205.7	220.3	182.2	147.2	215.1	209.9
Length range	189–283	126–290	110–331	87–347	120–347	123–400	119–350	134–435	118–396	124–287	129–325	105–370	109–251	138–412	101–354
Mean no. prey	14.6	27.8	19.0	17.0	37.4	10.8	9.4	12.0	17.1	16.0	13.7	21.9	17.4	12.3	19.2
Mean wt. prey	1.85	1.23	1.47	0.44	0.37	2.44	1.50	1.14	0.99	0.78	3.22	0.98	0.27	0.75	0.85

*Includes polychaetes, chaetognaths, gammarids, isopods, cumaceans, cirripedes, mysids, and gelatinous zooplankton.

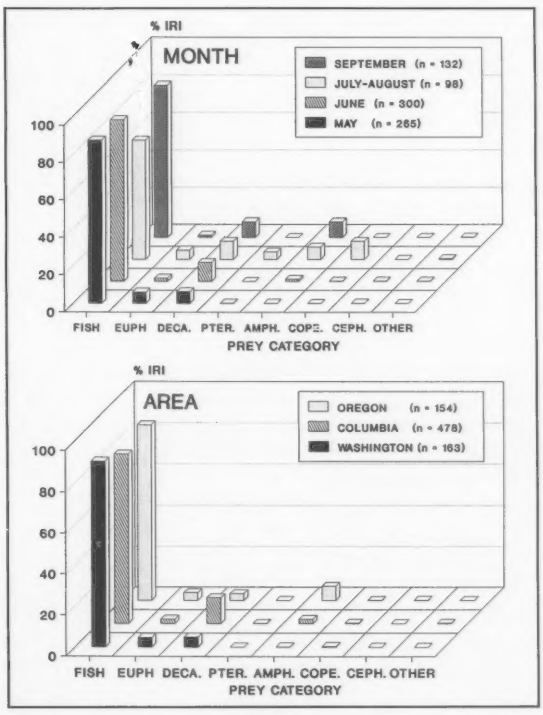

Figure 4
Juvenile chinook salmon diets by month and area for the major prey categories as a percent of total IRI. Sample sizes (no. of fish with food) for each subset are given in the legend. All figures include data collected off Washington and Oregon, 1980–85.

There were few consistent patterns observed among the invertebrate taxa consumed between the different areas (Fig. 4). Hyperiid amphipods were rarely found in chinook salmon stomachs collected off Washington as opposed to the other regions. The large numbers of decapod larvae eaten off the Columbia River were mainly *C. oregonensis* and *C. magister* larvae.

Chum salmon

General food habits Of the 109 chum salmon stomachs examined, 101 (92.6%) contained food; however, overall mean stomach fullness (2.4) and digestion (2.1) were low. The diet was dominated by zooplanktonic crustaceans, particularly euphausiids, calanoid copepods, and hyperiid amphipods (Appendix Table 2). Euphausiids (mostly juvenile *E. pacifica* and *T. spinifera*) accounted for over 54% of the total weight and 47% of the total IRI for all cruises combined. A taxonomically diverse array of hyperiids, copepods, and decapod larvae were also consumed. These taxa frequently occurred in the stomachs and were important numerically, but were of lesser importance gravimetrically. Chaetognaths and larvae and juveniles of several fish species were the dominant non-crustacean prey (Appendix Table 2).

Temporal variations Chum salmon diets varied considerably during the 5 years examined (Table 4). Some

Table 4

Summary of food habits by percent weight of major prey categories for juvenile chum salmon, by year, off Oregon and Washington.

	1981	1982	1983	1984	1985
Prey category					
Fishes	1.1	—	15.4	57.2	24.1
Euphausiids	78.3	60.7	20.5	13.7	33.0
Decapods	<0.1	8.6	1.0	—	2.0
Hyperiids	4.8	7.8	1.0	1.5	0.7
Pteropods	0.8	<0.1	—	—	—
Copepods	6.0	21.4	1.0	3.8	36.6
Chaetognaths	1.9	1.4	60.1	17.5	2.2
Other*	—	<0.1	0.9	6.1	1.3
Predator characteristics					
No. stomachs	24	33	15	8	29
No. empty	2	1	0	1	4
Mean length	190.6	161.6	116.2	165.4	132.2
Length range	108–237	97–223	103–133	126–214	115–155
Mean no. prey	47.4	8.0	78.1	20.1	83.4
Mean wt. prey	0.69	0.04	0.23	0.19	0.22

*Includes polychaetes, ostracods, mysids, insects, and larvaceans.

Table 5

Total number of prey taxa, Shannon-Weaver niche breadth (H′), maximun niche value (H'_{max}), and evenness (E) for each salmon species off Oregon and Washington, for all samples combined.

Species	Total number of prey taxa	H′	H'_{max}	E
Coho salmon	157	4.55	7.29	0.62
Chinook salmon	136	5.06	7.09	0.71
Chum salmon	51	4.35	5.67	0.77
Sockeye salmon	36	2.74	5.17	0.53

of this may be due to the months and areas sampled in different years. Euphausiids were the main food item by weight during 1981 and 1982. Although euphausiids were important during the later years, their contribution to the diet was less compared with chaetognaths, larval fishes, and calanoid copepods.

Sockeye salmon

General food habits The diet of juvenile sockeye salmon was similar to that of chum salmon. Juvenile euphausiids, calanoid copepods, chaetognaths, and fish larvae were consumed by the small number of fish examined (Appendix Table 2). Although a large number of prey taxa were identified, only a few were important. Among these were the euphausiid *T. spinifera*

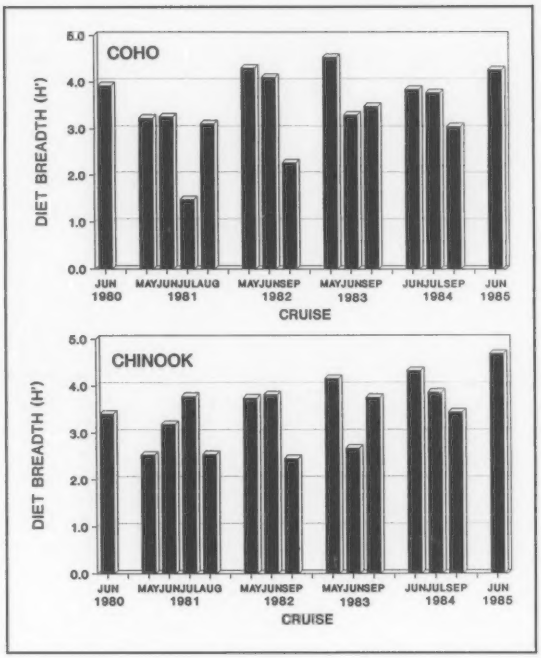

Figure 5

Shannon-Weaver niche breadth (H′) values for juvenile coho and chinook salmon for each cruise period.

and larval osmerid fishes. Chaetognaths were found in substantial numbers but were well digested and not identifiable to species. The relatively small sample size of sockeye salmon stomachs precluded a detailed analysis of diet variability.

All salmon species

Niche breadth Niche breadths, maximum possible niche breadths, and evenness values are given for each salmon species in Table 5. Chinook salmon had the highest overall diversity of prey taxa (H′ = 5.06), which was consistent with the high numbers of prey taxa found per stomach, and a high evenness ratio. Coho and chum salmon also consumed a diverse array of prey taxa, although coho stomachs frequently contained small numbers of prey items and showed low evenness overall. Chum salmon had a high diversity (H′ = 4.35), despite a substantial amount of unidentified and digested prey, and had the highest evenness (0.77) of all salmon species. The overall prey diversity of sockeye salmon was quite low (H′ = 2.74), which may be due in part to the small sample size and advanced state of digestion (mean digestion code = 2.0) of prey which prevented identification to lower taxonomic levels.

Table 6
Diet overlap by weight among all salmon species off Oregon and Washington, for all cruises combined.

Species	Coho	Chinook	Chum	Sockeye
Coho	—			
Chinook	54	—		
Chum	26	16	—	
Sockeye	25	24	33	—

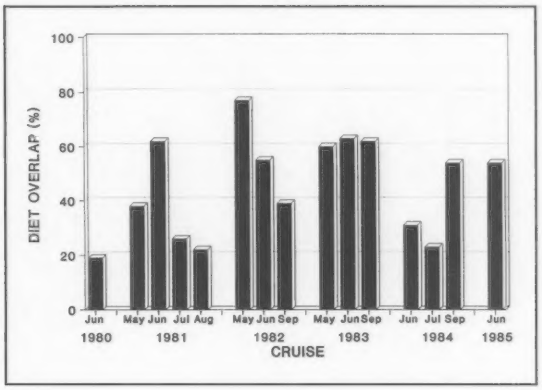

Figure 6
Diet overlap between juvenile coho and chinook salmon for each cruise period, 1980–85.

Table 7
Diet overlap by weight between juvenile coho and chinook salmon for collections off Oregon and Washington from which 10 stomachs of each species were examined. Also shown are the intraspecific overlap values for the same species at adjacent stations collected on the same day.

Date	Location	Distance offshore (km)	PSI Both	PSI Coho	PSI Chinook
1982					
June 1	45°00′, 124°05′	6.1	57		
1	44°41′, 124°24′	18.0	69		
7	47°00′, 124°25′	18.5	53		
8	46°41′, 124°18′	17.4	47	18	40
8	46°41′, 124°29′	31.8	49		
10	46°30′, 124°25′	27.6	45	38	31
10	46°30′, 124°18′	18.3	33		
1983					
Sept. 20	45°40′, 124°03′	8.9	91		
22	45°20′, 124°01′	3.7	62	59	61
22	45°17′, 124°01′	3.7	68		
1984					
June 8	47°00′, 124°25′	18.3	5		
1985					
June 18	46°19′, 124°11′	9.0	56		
25	47°40′, 124°53′	37.3	15		

Prey diversity varied greatly among cruises for juvenile coho (Fig. 5). Generally lower values occurred during 1981, especially in July, when pteropods were very important in the diet. Coho salmon had higher diversity values in 1983 and 1984 than in 1981. Chinook salmon showed many of the same interannual and seasonal trends in prey diversity as coho salmon, except that prey diversity was not appreciably lower in 1981 (Fig. 5).

Dietary overlap Diet overlap by weight among the salmon species for all cruises combined was generally low, with none of the six species pairs showing significant (>60%) overlap (Table 6). The diets of juvenile coho and chinook salmon were most similar (PSI = 54%), reflecting their common foraging on many of the same euphausiid, larval decapod, and fish species. Chum salmon diets showed the least similarity to the other species, which may be a function of the poor digestive state of the stomach contents of this species.

To examine the finer-scale variability in diet similarity between coho and chinook salmon juveniles, diet overlap was calculated for each cruise month (Fig. 6). With the exception of 1983, which showed the highest overall similarity, monthly overlap values were highly variable within years containing more than one cruise. No consistent patterns were observed between years for the same months.

A wide range of diet overlap values was observed for the 13 collections from which 10 stomachs of coho and chinook were analyzed (Table 7). Overlap was highest in the collections from September 1983, due mainly to the common utilization of *E. mordax* and several hyperiid amphipod species. Intermediate overlaps were generally observed during June 1982, resulting mainly from consumption of the same euphausiid species by both predators. There appeared to be no relationship between diet overlap and the inshore-offshore location of the collection. Diet overlap between juvenile coho and chinook at a particular station was generally higher than intraspecific overlap for either species at adjacent stations (Table 7).

Analysis of dietary variations The contingency table analysis for presence or absence of the four most-commonly-occurring major prey categories showed that there were generally highly significant variations ($P \leq 0.001$) in diets of coho and chinook juveniles by

Table 8

Results of the chi-square analysis analyzing each factor independently of the other two for major prey categories of juvenile coho and chinook salmon off Oregon and Washington. Degrees of freedom are in parentheses below each factor.

Prey category	Year† (3)	Month (3)	Area (2)
Coho salmon			
Fishes	75.32***	83.38***	51.54***
Euphausiids	31.19***	106.38***	10.71**
Decapods	39.48***	38.42***	7.80*
Amphipods	74.61***	53.21***	2.79 n.s.
Chinook salmon			
Fishes	68.25***	65.95***	2.51 n.s.
Euphausiids	33.03***	3.15 n.s.	15.48***
Decapods	46.92***	49.15***	5.96 n.s.
Amphipods	14.36**	60.71***	13.15**

*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$, n.s. $P > 0.05$
†Tested for 1981–84 only.

Table 9

Results of the chi-square analysis analyzing inshore-offshore variations for major prey categories of juvenile coho and chinook salmon off Oregon and Washington. All significances are at 2 degrees of freedom.

Prey category	Coho salmon		Chinook salmon	
	May 81	June 84	May 82	June 85
Fishes	3.86 n.s.	5.82 n.s.	1.34 n.s.	1.40 n.s.
Euphausiids	3.14 n.s.	2.66 n.s.	1.82 n.s.	9.76**
Decapods	3.83 n.s.	15.07***	9.00*	1.82 n.s.
Amphipods	3.14 n.s.	15.88***	3.23 n.s.	0.41 n.s.

*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$, n.s. $P > 0.05$

year and month (Table 8). The only comparison which showed non-significant variation by year or month was the monthly variation in euphausiid occurrences for juvenile chinook salmon. Three prey categories did not show significant variation ($P > 0.05$) when analyzed by area. Comparisons by area showed less significant variation than by year and month for both coho and chinook salmon juveniles for most of the major prey categories (Table 8).

Examination of inshore-offshore variations in major prey composition for four cruises (two each for coho and chinook salmon) showed generally few significant variations by occurrence for the dominant prey categories (Table 9). Although the species and life-history-stage composition of the prey was different in inshore and offshore collections (i.e., more *Sebastes* and *Engraulis* larvae offshore, and more juvenile *Ammodytes*, *Clupea*, and *Hemilepidotus* inshore), all cross-shelf variations in total fish occurrences were not significant ($P > 0.05$). The most significant differences were for decapod larvae, and were due to higher occurrences of *Cancer* spp. megalopae in chinook salmon stomachs inshore in May 1982 and lower occurrences in coho salmon stomachs inshore in June 1984.

Discussion

Overall food habits

This study represents the first detailed description of the diets of several species of sympatric juvenile salmon in coastal marine waters off Washington and Oregon. Despite generally low diet overlaps at the lowest taxonomic levels, there were some similarities in the major prey groups consumed by the salmon species. Juvenile chinook salmon were primarily piscivorous, consuming a variety of larval and juvenile fishes. The diet of coho salmon consisted of both fishes and large zooplanktonic crustaceans, such as euphausiids, crab megalopae, and hyperiid amphipods. Chum and sockeye salmon diets were more diverse than the diets of coho and chinook salmon, with fishes, small crustaceans (euphausiid furcilia and juveniles, crab larvae, and copepods), and chaetognaths being important prey.

Our findings are consistent with what is known of the marine food habits of juvenile salmon off Washington and Oregon and British Columbia. Juvenile chinook salmon tend to be more piscivorous than juvenile coho for the same-sized predator (Healey 1978, 1980; Peterson et al. 1982; Emmett et al. 1986). Coho collected during this study, however, consumed a larger overall mean length of fish prey relative to predator length (Brodeur In press). Juvenile northern anchovy, Pacific sand lance, and rockfishes were the dominant fish species eaten off Washington and Oregon (Peterson et al. 1982, Emmett et al. 1986), and herring and Pacific sand lance were the main fish species consumed off British Columbia (Healey 1978, 1980). Many of these prey fish species tend to be heavily pigmented and are often associated with the neustonic layer in coastal waters (Brodeur et al. 1987b, Shenker 1988, Brodeur 1989).

Macrozooplankton, such as euphausiids, hyperiid amphipods, and crab larvae, are also readily consumed by these juvenile salmon. These macrozooplankton prey may be easily detected due to their large size or darkly-pigmented eyes (Peterson et al. 1982) and occur in large aggregations near the surface (Brodeur et al. 1987b, Shenker 1988). Terrestrial insects, which may be blown

to sea in large numbers during favorable meteorological conditions, can also contribute substantially to the diets of juvenile coho salmon and other salmonids (Brodeur 1989).

Fishes were much less important in the diets of juvenile chum and sockeye salmon; however, the mean and maximum size of the individuals of these species examined in this study were smaller than those of coho and chinook salmon. Juvenile euphausiids were a major component in the diet of chum and sockeye salmon in this study. Peterson et al. (1982) found juvenile euphausiids were a major prey of chum juveniles off Oregon, whereas copepods, larvaceans, and hyperiid amphipods were most important off British Columbia (Manzer 1969; Healey 1978, 1980). Both chum and sockeye consumed a greater number of chaetognaths than coho and chinook, and the importance of these and other soft-bodied prey may be greatly underestimated in most studies because they are probably digested very rapidly in salmon stomachs (Black and Low 1983).

Patterns in dietary variability

The pronounced interannual differences in the diets of most species were expected, even when the collections from same months and areas were examined. Oceanographic conditions varied greatly among the years, with both relatively strong (1982 and 1985), weak (1983 and 1984), and highly variable (1981) upwelling occurring during the study period (Fisher and Pearcy 1988). In addition, a strong El Niño event dominated ocean conditions in coastal waters of the northeast Pacific during the summer months of 1983 and 1984, greatly affecting primary and secondary productivity and fish production (Mysak 1986, Pearcy and Schoener 1987).

Fish prey, as a proportion of the total diet by weight, was generally invariant for the same months among the different years. However, the species composition alternated between coastal and offshore taxa (as identified by Richardson and Pearcy [1977]) depending on the prevalent hydrographic regime in the various years. Several coastal taxa (*Ammodytes hexapterus*, *Clupea harengus pallasi*, *Hemilepidotus spinosus*, and Osmeridae) were more prevalent during strong upwelling years, whereas offshore taxa (*Engraulis mordax*, *Sebastes* spp., *Ronquilus jordani*, and pleuronectid larvae) were eaten more frequently during poor upwelling years. Although ichthyoplankton collections were not made during every year of the stomach sampling, one limited study lends support to our diet observations. In a series of plankton tows along one transect off the central Oregon coast in 1983, Brodeur et al. (1985) found high abundances of offshore fish taxa at inshore stations compared with past studies. The larvae of the northern anchovy were unusually abundant that year, and juvenile anchovy made up the majority of the diet-by-weight of juvenile coho and chinook salmon during September 1983. Osmerid larvae, generally the dominant larvae inshore off Oregon (Richardson and Pearcy 1977), were found in low abundance in both the plankton collections and fish stomachs during 1983.

Several invertebrate taxa showed substantial interannual variation. The pteropod *L. helicina* was one of the most important prey consumed in 1981, but was relatively unimportant in other years. The dominant inshore euphausiid *T. spinifera* was extremely abundant in the stomachs following periods of active upwelling, but was rarely consumed during the El Niño of 1983 and early 1984 (Brodeur 1986). Several species of decapod larvae were present in greater numbers in the diets of all salmon species during 1983 and early 1984. Many other El Niño-related anomalies that were observed in the diet of coho salmon during 1983 were described by Pearcy et al. (1985). The diets of coho salmon during 1984 showed above-average abundances of terrestrial insects, which presumably were blown offshore by anomalous winds during the summer of 1984 (Brodeur 1989).

Strong seasonal variations in feeding habits of juvenile coho and chinook salmon were evident in the years that had multiple cruises over the 5-month sampling period. Some of the variability may have been due to the seasonal increase in the mean size of the salmon, which allowed a greater size range of prey to be consumed later in the summer (Brodeur In press). However, much of the diet variation may have been due to seasonal variations in the abundance of meroplanktonic prey (e.g., decapod and fish larvae). The timing and duration of spawning, larval development, and settlement to benthic juvenile habitat are relatively fixed for most meroplanktonic species (Lough 1975, Richardson and Pearcy 1977, Parrish et al. 1981) such that their seasonal occurrence in the plankton and the diets of juvenile salmon are relatively predictable. Exceptions may occur during anomalous years such as during an El Niño (Bailey and Incze 1985, Brodeur et al. 1985). Several of the major holoplanktonic taxa (e.g., euphausiids, hyperiids, and pteropods) also showed a consistent seasonal succession of developmental stages, but many species were present throughout the summer period (Brodeur 1990).

It was not surprising that geographic (north-south) variations in the diet composition of most salmon species were not as substantial as temporal variations, because most of the prey species are distributed throughout the range of latitudes we sampled. Similar results were found for adult salmonids and nonsalmonid species by Brodeur et al. (1987a). However, oceanographic regimes may be quite variable between

regions (Brodeur and Pearcy 1986), which could result in different feeding conditions for juvenile salmonids within each region. The Columbia River region may be quite different hydrographically and biologically from the upwelling regions off Washington and Oregon due to the presence of a warm, low-salinity plume extending over much of the Columbia River area during the summer. Oceanic species (e.g., *Sebastes* spp., *E. pacifica*) rarely occurred in the stomachs collected from the Columbia region, whereas *E. mordax*, a species whose northern subpopulation spawns within the relatively stable Columbia River plume (Richardson 1980), was generally well represented in salmon stomachs collected in this region.

The relatively minor cross-shelf variations in the major prey taxa consumed by coho and chinook were not expected, considering that many studies have found substantial variations in cross-shelf species distributions (Peterson and Miller 1976, Richardson and Pearcy 1977, Richardson et al. 1980, Shenker 1988). However, the frequency of occurrence of major prey may not be a representative measure of the diet from a particular area. The larvae of many meroplanktonic taxa (e.g., *Sebastes* spp., *Hemilepidotus* spp., and *Cancer* spp.) are generally found offshore and progressively migrate or are transported inshore as they grow prior to settling to an inshore benthic habitat as juveniles (Richardson et al. 1980, Shenker 1988). Euphausiids consumed in our inshore study area were mainly *T. spinifera*, whereas *E. pacifica* were consumed in the offshore area. These euphausiid species have little overlap in distribution (Hebard 1966). Hyperiid amphipods were also represented by an inshore species, *Hyperoche medusarum*, and an offshore species, *T. pacifica* (Lorz and Pearcy 1975). These and other cross-shelf species differences were not detectable when analyzing stomach contents at higher taxonomic levels. However, species-level distinctions may be irrelevant to a foraging predator, if the size, energy content, and behavior of both prey species are similar.

The high prey-diversity and generally high niche-breadth values agree with previous studies which indicate that many of these salmon species are not specialists in their oceanic feeding modes, but rather consume any available prey within the proper size-range. Many of the same geographic, interannual, and seasonal patterns found in the feeding habits of the adult salmonids and pelagic nonsalmonid species (Brodeur et al. 1987a) were found in our study. These similar patterns suggest that the zooplankton and ichthyoplankton population cycles, which are intricately coupled to seasonal production cycles, may be important determinants of the feeding ecology of these salmon species. The ability to switch to alternate prey, when preferred prey are limiting, may be an important factor in the marine survival of salmon.

The high overlaps between coho and chinook juveniles seen for some cruises or individual collections may signify that some competition for prey may be occurring. This interaction could be particularly acute since coho and chinook exhibit a high degree of spatial overlap in their distributions (Pearcy and Fisher In press). This would be conceivable only if prey resources were limiting.

Because of the highly opportunistic feeding mode of most salmonids and the substantial heterogeneity in the physical and biological environment, a large-scale study over extended time-periods may be necessary to adequately describe the feeding dynamics of juvenile salmon. Major departures from the long-term mean oceanographic conditions, as exemplified by an El Niño event, can strongly affect the feeding ecology of many pelagic planktivores. Fulton and LeBrasseur (1985) have hypothesized that a northward shifting of the Subarctic Boundary from its normal position intersecting the coast off Oregon or northern California to well above Vancouver Island, British Columbia, as occurs in El Niño conditions, may expose salmon and other pelagic predators to a novel suite of available prey, with a corresponding downward shift in prey size. Grover and Olla (1987) found that a smaller mean size of copepod was consumed by larval sablefish *Anoplopoma fimbria* during the El Niño year of 1983 than during 1980, a year of relatively normal oceanographic conditions.

Our study also demonstrated anomalies in species composition in the diet during 1983 and early 1984 compared with other years; relatively large northern euphausiids were replaced by much smaller decapod larvae (i.e., Graspidae, Porcellanidae, and Pinnotheridae) and euphausiids (*Nyctiphanes simplex*) of southern origin (Brodeur 1986). Similar interannual shifts were seen in the fish prey-size spectrum consumed by coho and chinook salmon juveniles with generally smaller prey consumed during 1983 and 1984 (Brodeur In press). Consumption of smaller prey must be balanced by consumption of a greater number of prey of equivalent caloric content in order to maintain the similar growth rates seen for coho salmon during the early summers of 1983 and 1984 as non-Niño years (Fisher and Pearcy 1988). Unless prey are more aggregated during El Niño years, smaller prey would require a substantial increase in time and energy spent foraging, relative to time spent avoiding predators. This increased foraging time, at the expense of predator avoidance, may have led to the low coho and chinook salmon survival in the ocean during the El Niño years (Johnson 1988).

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Appendix Table 1

Percent frequency occurrence (F), percent number (N), percent weight (W), and percent index of relative importance (IRI) of food items in juvenile coho and chinook salmon stomachs taken off Oregon and Washington, for all years combined. Numbers in parentheses refer to summaries for major taxonomic groupings.

	Coho salmon				Chinook salmon			
Prey taxa	F	N	W	IRI	F	N	W	IRI
Cnidaria								
Velella velella	0.3	<0.1	<0.1	<0.1	–	–	–	–
Ctenophora								
Unidentified	<0.1	<0.1	<0.1	<0.1	0.5	<0.1	<0.1	<0.1
Siphonophora								
Unidentified	1.0	<0.1	<0.1	<0.1	0.5	<0.1	<0.1	<0.1
Annelida								
Tomopteris septentrionalis	<0.1	<0.1	<0.1	<0.1	–	–	–	–
Tomopteris sp.	0.6	0.1	<0.1	<0.1	–	–	–	–
Pelagobia sp.	0.1	<0.1	<0.1	<0.1	–	–	–	–
Nereidae	–	–	–	–	0.1	<0.1	0.1	<0.1
Unidentified	0.5	<0.1	<0.1	<0.1	0.1	0.2	<0.1	<0.1
Mollusca								
Gastropoda	(18.4)	(13.4)	(5.9)		(4.1)	(1.3)	(0.3)	
Limacina helicina	16.5	13.0	5.5	10.4	4.0	1.3	0.3	0.3
Euclio pyramidata	1.5	0.3	0.5	<0.1	–	–	–	–
Clio limacina	0.1	0.1	<0.1	<0.1	–	–	–	–
Pteropoda unidentified	0.4	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Cephalopoda	(2.0)	(0.1)	(0.9)		(2.0)	(0.4)	(1.5)	
Loligo opalescens	1.0	0.1	0.8	<0.1	0.7	0.4	1.1	<0.1
Abraliopsis sp.	0.1	<0.1	<0.1	<0.1	–	–	–	–
Gonatidae	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Octopus dofleini	–	–	–	–	0.2	<0.1	0.1	<0.1
Unidentified	0.8	<0.1	0.1	<0.1	0.9	<0.1	0.2	<0.1
Arthropoda								
Copepoda	(9.6)	(2.1)	(0.2)		(8.5)	(2.6)	(0.2)	
Gaussia princeps	–	–	–	–	0.1	<0.1	<0.1	<0.1
Neocalanus cristatus	3.2	0.5	0.1	<0.1	3.8	0.7	0.1	0.1
Neocalanus plumchrus	0.5	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Calanus marshallae	0.5	<0.1	<0.1	<0.1	0.2	0.1	<0.1	<0.1
Calanus pacificus	1.7	0.5	<0.1	<0.1	0.4	1.2	<0.1	0.1
Calanus spp. copepodites	0.6	0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Eucalanus bungii	0.3	0.6	<0.1	<0.1	0.9	0.2	<0.1	<0.1
Metridia pacifica	0.2	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Epilabidocera longipedata	1.6	0.1	<0.1	<0.1	0.6	<0.1	<0.1	<0.1
Euchaeta elongata	0.1	<0.1	<0.1	<0.1	–	–	–	–
Eurytemora americana	0.1	<0.1	<0.1	<0.1	–	–	–	–
Candacia bipinnata	0.1	<0.1	<0.1	<0.1	–	–	–	–
Unidentified	3.4	0.2	<0.1	<0.1	2.6	0.3	<0.1	<0.1
Cirripedia								
Unidentified cypris	1.7	0.1	<0.1	<0.1	0.4	<0.1	<0.1	<0.1
Unidentified remains	0.2	<0.1	<0.1	<0.1	–	–	–	–
Mysidacea								
Acanthomysis macropsis	0.1	<0.1	<0.1	<0.1	1.0	<0.1	<0.1	<0.1
Neomysis kadiakensis	0.5	0.1	<0.1	<0.1	1.0	0.1	0.1	<0.1
Mysidopsis californica	0.1	<0.1	<0.1	<0.1	–	–	–	–
Unidentified	0.3	<0.1	<0.1	<0.1	0.5	0.3	<0.1	<0.1
Cumacea								
Eudorella sp.	–	–	–	–	0.1	0.2	<0.1	<0.1
Unidentified	<0.1	<0.1	<0.1	<0.1	–	–	–	–
Isopoda								
Synidotea bicuspida	–	–	–	–	0.1	0.2	<0.1	<0.1
Gnorimosphaeroma oregonensis	–	–	–	–	0.1	<0.1	<0.1	<0.1
Idotea fewkesi	0.2	<0.1	<0.1	<0.1	–	–	–	–

Appendix Table 1 (continued)

Prey taxa	Coho salmon F	Coho salmon N	Coho salmon W	Coho salmon IRI	Chinook salmon F	Chinook salmon N	Chinook salmon W	Chinook salmon IRI
Arthropoda (continued)								
Amphipoda	(42.0)	(22.3)	(3.1)		(20.7)	(9.6)	(0.4)	
Atylus tridens	2.5	1.9	<0.1	0.2	2.5	2.1	<0.1	0.2
Calliopius laeviusculus	0.2	0.3	<0.1	<0.1	–	–	–	–
Cyphocaris challengeri	–	–	–	–	0.1	<0.1	<0.1	<0.1
Unidentified Gammaridea	0.3	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Hyperia medusarum	5.8	1.1	0.2	0.3	2.3	<0.1	0.1	<0.1
Hyperia spinigera	0.1	<0.1	<0.1	<0.1	0.1	0.2	<0.1	<0.1
Hyperoche medusarum	27.6	13.4	1.6	13.9	12.4	6.7	0.2	3.6
Themisto pacifica	13.7	4.2	0.6	2.2	1.9	<0.1	<0.1	<0.1
Primno brevidens	0.5	<0.1	<0.1	<0.1	–	–	–	–
Primno macropa	0.6	<0.1	<0.1	<0.1	1.5	<0.1	<0.1	<0.1
Phronima sedentaria	1.5	0.1	0.1	<0.1	0.9	<0.1	<0.1	<0.1
Paraphronima crassipes	0.3	<0.1	<0.1	<0.1	–	–	–	–
Paraphronima gracilis	0.5	0.1	<0.1	<0.1	–	–	–	–
Vibilia armata	3.6	0.2	<0.1	<0.1	1.0	<0.1	<0.1	<0.1
Vibilia australis	1.3	0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Vibilia propinquus	3.1	0.1	0.1	<0.1	0.2	<0.1	<0.1	<0.1
Vibilia pyripes	0.2	<0.1	<0.1	<0.1	–	–	–	–
Vibilia viatrix	1.7	0.1	0.1	<0.1	0.1	<0.1	<0.1	<0.1
Vibiliidae unidentified	0.8	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Streetsia challengeri	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Oxycephalus clausi	0.2	<0.1	<0.1	<0.1	–	–	–	–
Lestrigonus schizogeniosis	0.1	<0.1	<0.1	<0.1	–	–	–	–
Brachyscelus crusculum	0.5	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Unidentified Hyperiidea	10.6	0.8	0.4	0.4	3.9	0.5	<0.1	0.1
Caprella incisa	0.1	<0.1	<0.1	<0.1	–	–	–	–
Caprella verrucosa	0.1	<0.1	<0.1	<0.1	–	–	–	–
Euphausiacea	(33.7)	(15.6)	(10.2)		(18.2)	(13.0)	(4.7)	
Euphausia pacifica	10.0	1.6	3.9	1.9	2.8	0.8	0.8	0.2
Nematoscelis difficilis	0.2	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Thysanoessa spinifera	19.5	11.6	5.1	11.0	11.1	10.3	3.5	6.4
Nyctiphanes simplex	3.0	0.4	0.2	0.1	1.6	0.1	<0.1	<0.1
Unidentified furcilia	1.3	1.0	<0.1	<0.1	0.6	<0.1	<0.1	<0.1
Unidentified	11.8	1.0	1.0	0.8	5.5	1.7	0.3	0.5
Decapoda	(45.1)	(28.2)	(4.8)		(35.0)	(29.1)	(3.3)	
Hippolyte clarki	0.1	<0.1	<0.1	<0.1	–	–	–	–
Hippolytidae unidentified	0.2	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Pandalus jordani	–	–	–	–	2.3	0.4	0.1	<0.1
Pandalus spp. zoea	0.3	<0.1	<0.1	<0.1	1.6	1.4	<0.1	0.1
Crangon spp. zoea	3.1	1.0	0.1	0.1	5.2	1.1	0.1	0.3
Natantia unidentified	0.5	0.1	<0.1	<0.1	0.5	<0.1	<0.1	<0.1
Callianassa sp. zoea	0.6	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Upogebia sp. zoea	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Emerita analoga	0.2	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Pagurus granosimanus	0.1	<0.1	<0.1	<0.1	–	–	–	–
Pagurus spp. zoea	0.9	<0.1	<0.1	<0.1	0.6	<0.1	<0.1	<0.1
Pagurus spp. megalopae	4.4	1.0	0.1	0.2	2.6	2.4	<0.1	0.3
Petrolithes cinctipes	0.2	<0.1	<0.1	<0.1	–	–	–	–
Petrolithes eriomerus	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Pachycheles pubescens	0.6	<0.1	<0.1	<0.1	0.7	0.2	<0.1	<0.1
Pachycheles rudis	0.5	0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Pachycheles sp. zoea	0.2	<0.1	<0.1	<0.1	0.4	0.1	<0.1	<0.1
Porcellanidae zoea	1.4	0.1	<0.1	<0.1	0.6	0.2	<0.1	<0.1
Porcellanidae megalopae	2.5	0.4	<0.1	<0.1	2.6	0.7	<0.1	0.3
Oregonia gracilis	0.5	<0.1	<0.1	<0.1	0.2	0.2	<0.1	<0.1
Chionoecetes tanneri	0.2	<0.1	<0.1	<0.1	0.6	<0.1	<0.1	<0.1
Pugettia producta zoea	3.2	0.1	<0.1	<0.1	3.1	0.3	<0.1	<0.1

Appendix Table 1 (continued)

Prey taxa	Coho salmon F	Coho salmon N	Coho salmon W	Coho salmon IRI	Chinook salmon F	Chinook salmon N	Chinook salmon W	Chinook salmon IRI
Arthropoda (continued)								
Decapoda (continued)								
Cancer antennarius megalopae	3.6	1.0	<0.1	0.1	2.5	1.3	0.3	0.2
Cancer magister megalopae	8.0	1.1	1.0	0.6	6.0	2.5	1.4	1.0
Cancer oregonensis megalopae	24.2	13.2	2.2	12.5	13.8	8.0	0.6	5.0
Cancer spp. zoea	8.6	5.5	0.3	1.7	1.9	0.6	<0.1	<0.1
Cancer spp. megalopae	4.1	0.4	0.2	0.1	3.3	0.3	0.2	0.1
Fabia subquadrata	0.8	0.1	<0.1	<0.1	1.1	3.3	0.1	0.2
Pinnixia sp. megalopae	0.2	<0.1	<0.1	<0.1	—	—	—	—
Pinnotheridae zoea	5.7	2.7	0.3	0.6	4.0	2.7	0.1	0.5
Pinnotheridae megalopae	2.0	0.3	0.1	<0.1	3.9	2.0	0.1	0.3
Lophopanopeus bellus	2.9	0.4	<0.1	<0.1	0.7	0.1	<0.1	<0.1
Pachygraspus crassipes	0.1	<0.1	<0.1	<0.1	—	—	—	—
Hemigraspus oregonensis	0.2	<0.1	<0.1	<0.1	—	—	—	—
Unidentified larvae	3.6	0.1	<0.1	<0.1	2.6	0.7	0.1	0.1
Unidentified Crustacea	3.2	<0.1	0.2	<0.1	1.1	<0.1	<0.1	<0.1
Insecta	(6.9)	(1.4)	(0.9)		(3.1)	(0.6)	(0.1)	
Psocoptera	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Hemiptera	0.2	<0.1	<0.1	<0.1	—	—	—	—
Cicadellidae	—	—	—	—	0.1	<0.1	<0.1	<0.1
Aphididae	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Homoptera	0.2	<0.1	<0.1	<0.1	—	—	—	—
Coccinellidae	0.1	<0.1	<0.1	<0.1	—	—	—	—
Coleoptera	0.1	<0.1	<0.1	<0.1	—	—	—	—
Hemerobiidae	0.9	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Neuroptera	0.2	<0.1	<0.1	<0.1	—	—	—	—
Choristoneura occidentalis	1.3	0.4	0.8	0.1	—	—	—	—
Geometridae	0.1	<0.1	<0.1	<0.1	—	—	—	—
Lepidoptera	0.4	0.1	<0.1	<0.1	—	—	—	—
Nematocera	0.5	<0.1	<0.1	<0.1	—	—	—	—
Brachycera	0.6	<0.1	<0.1	<0.1	0.4	<0.1	<0.1	<0.1
Chironomid larvae	—	—	—	—	0.1	0.1	<0.1	<0.1
Diptera	0.5	<0.1	<0.1	<0.1	0.2	0.2	<0.1	<0.1
Formicidae	—	—	—	—	0.1	<0.1	<0.1	<0.1
Hymenoptera	0.1	0.1	<0.1	<0.1	0.1	0.2	<0.1	<0.1
Unidentified	4.1	0.7	0.1	0.1	2.4	0.1	<0.1	<0.1
Chaetognatha								
Eukhronia hamata	—	—	—	—	0.1	<0.1	<0.1	<0.1
Sagitta elegans	0.3	0.6	<0.1	<0.1	—	—	—	—
Unidentified	1.2	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Salpidae								
Unidentified	0.4	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Chordata								
Osteichthyes	(66.7)	(15.2)	(72.0)		(85.3)	(42.1)	(88.3)	
Clupea harengus pallasi	3.4	0.1	2.5	0.3	6.3	0.3	1.8	0.5
Engraulis mordax	7.4	0.4	23.3	5.9	12.2	2.0	34.9	18.9
Allosmerus elongatus	0.2	<0.1	0.7	<0.1	0.9	<0.1	2.0	0.1
Spirinchus starksi	—	—	—	—	0.1	<0.1	0.4	<0.1
Osmeridae unidentified	3.4	0.7	1.3	0.2	5.8	0.5	2.9	0.8
Myctophidae unidentified	0.2	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Gadus macrocephalus	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Microgadus proximus	1.7	0.1	1.6	0.1	1.8	0.7	0.6	0.1
Sebastes jordani	0.2	<0.1	0.3	<0.1	0.2	<0.1	0.3	<0.1
Sebastes spp.	14.7	2.6	13.0	7.7	11.7	2.9	8.4	5.5
Hexagrammos decagrammus	0.1	<0.1	0.1	<0.1	0.1	<0.1	<0.1	<0.1
Hexagrammos spp.	0.3	<0.1	0.3	<0.1	—	—	—	—
Ophiodon elongatus	0.5	<0.1	0.2	<0.1	0.6	<0.1	0.1	<0.1
Hexagrammidae unidentified	1.1	0.1	0.9	<0.1	0.4	<0.1	0.1	<0.1

Appendix Table 1 (continued)

Prey taxa	Coho salmon F	Coho salmon N	Coho salmon W	Coho salmon IRI	Chinook salmon F	Chinook salmon N	Chinook salmon W	Chinook salmon IRI
Chordata (continued)								
Osteichthyes (continued)								
Agonopsis vulsa	–	–	–	–	0.1	<0.1	<0.1	<0.1
Odontopyxis trispinosa	–	–	–	–	1.5	0.2	<0.1	<0.1
Stellerina xyosterna	–	–	–	–	0.1	<0.1	<0.1	<0.1
Agonidae unidentified	0.1	0.1	<0.1	<0.1	0.9	<0.1	<0.1	<0.1
Cyclopteridae unidentified	0.1	0.1	<0.1	<0.1	0.6	<0.1	0.1	<0.1
Artedius fenestralis	0.1	0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Artedius harringtoni	–	–	–	–	0.6	<0.1	<0.1	<0.1
Artedius meanyi	0.1	<0.1	<0.1	<0.1	1.0	<0.1	<0.1	<0.1
Hemilepidotus spinosus	5.8	0.2	2.2	0.5	14.0	0.8	6.8	4.5
Radulinus asprellus	0.1	<0.1	<0.1	<0.1	0.5	0.2	<0.1	<0.1
Scorpaenichthys marmoratus	0.8	0.1	0.1	<0.1	0.1	<0.1	<0.1	<0.1
Chitonotus pugetensis	0.1	<0.1	<0.1	<0.1	0.2	0.2	<0.1	<0.1
Cottidae unidentified	1.3	<0.1	0.2	<0.1	4.1	3.5	0.4	0.7
Ammodytes hexapterus	9.5	2.7	4.4	2.3	13.7	4.4	4.3	5.1
Pholidae unidentified	0.1	0.1	<0.1	<0.1	–	–	–	–
Ronquilus jordani	1.6	0.8	0.6	0.1	2.5	4.5	0.4	0.5
Stichaeidae unidentified	0.1	<0.1	<0.1	<0.1	–	–	–	–
Coryphopterus nicholsi	0.1	<0.1	<0.1	<0.1	–	–	–	–
Citharichthys sordidus	0.1	<0.1	<0.1	<0.1	0.4	<0.1	0.1	<0.1
Citharichthys stigmaeus	0.2	<0.1	0.1	<0.1	1.0	<0.1	0.7	<0.1
Atherestes stomias	–	–	–	–	1.0	2.8	0.5	0.1
Eopsetta jordani	–	–	–	–	0.1	<0.1	<0.1	<0.1
Glyptocephalus zachirus	0.4	<0.1	<0.1	<0.1	1.0	<0.1	0.3	<0.1
Hippoglossoides elassodon	–	–	–	–	0.1	<0.1	<0.1	<0.1
Isopsetta isolepis	0.5	<0.1	<0.1	<0.1	3.6	0.2	0.6	0.1
Lepidopsetta bilineata	–	–	–	–	0.1	<0.1	<0.1	<0.1
Lyopsetta exilis	–	–	–	–	0.6	<0.1	0.1	<0.1
Parophrys vetulus	0.4	<0.1	0.1	<0.1	3.3	0.1	0.4	0.1
Psettichthys melanostictus	1.5	0.1	0.5	<0.1	6.7	1.6	1.9	1.0
Pleuronectidae larvae	1.6	<0.1	0.3	<0.1	7.7	0.4	1.1	0.5
Unidentified larvae	8.9	1.3	1.1	0.7	18.7	5.1	3.5	6.8
Unidentified juveniles	4.4	1.7	2.9	0.7	6.2	2.5	4.8	1.9
Unidentified remains	38.0	3.4	14.5	22.9	41.5	8.3	10.2	32.3
Plant material	3.0	0.4	0.2	0.1	1.3	<0.1	<0.1	<0.1
Unidentified material	16.9	0.2	1.2	0.8	9.1	0.1	0.7	0.3
Number of stomachs examined		1652				844		
Number of empty stomachs		79				49		
Mean fork length (mm)		193.80				200.47		
Fork length range (mm)		81–421				81–435		

Appendix Table 2

Percent frequency occurrence (F), percent number (N), percent weight (W), and percent index of relative importance (IRI) of food items in juvenile chum and sockeye salmon stomachs taken off Oregon and Washington, for all years combined. Numbers in parentheses refer to summaries for major taxonomic groupings.

	Chum salmon				Sockeye salmon			
Prey taxa	F	N	W	IRI	F	N	W	IRI
Cnidaria								
Velella velella	1.0	<0.1	0.1	<0.1	–	–	–	–
Siphonophora								
Unidentified	2.0	0.2	0.1	<0.1	–	–	–	–
Annelida								
Tomopteris spp.	–	–	–	–	16.7	0.3	2.2	1.0
Unidentified	2.0	0.3	<0.1	<0.1	–	–	–	–
Mollusca								
Gastropoda								
Limacina helicina	3.0	0.1	0.5	0.1	16.7	1.5	2.5	1.7
Arthropoda								
Ostracoda								
Unidentified	1.0	<0.1	<0.1	<0.1	–	–	–	–
Copepoda	(49.0)	(39.2)	(11.5)		(46.7)	(11.0)	(5.1)	
Calanus marshallae	4.9	0.1	0.3	0.1	3.3	<0.1	0.1	<0.1
Calanus pacificus	12.9	7.4	3.1	4.7	3.3	7.6	2.1	0.8
Calanus spp. copepodites	3.0	1.0	0.4	0.1	3.3	<0.1	0.1	<0.1
Neocalanus cristatus	10.9	2.3	1.8	1.6	10.0	0.1	0.3	0.1
Neocalanus plumchrus	7.9	0.6	0.5	0.3	20.0	1.3	0.6	1.0
Eucalanus bungii	13.9	17.0	3.8	10.0	–	–	–	–
Epilabidocera longipedata	1.0	0.8	0.1	<0.1	6.7	0.3	0.2	0.1
Unidentified	20.8	10.3	1.9	8.8	26.7	1.6	1.5	2.0
Cirripedia								
Unidentified cypris	3.0	<0.1	0.1	<0.1	–	–	–	–
Mysidacea								
Acanthomysis macropsis	1.0	0.3	0.1	<0.1	–	–	–	–
Amphipoda	(46.1)	(5.8)	(7.8)		(46.7)	(2.7)	(3.6)	
Hyperia medusarum	1.0	0.6	<0.1	<0.1	–	–	–	–
Hyperoche medusarum	27.7	2.4	3.1	5.3	36.7	1.4	2.0	3.0
Themisto pacifica	7.9	2.3	0.3	0.7	13.3	0.4	0.3	0.2
Primno macropa	1.0	0.3	<0.1	<0.1	–	–	–	–
Vibilia armata	1.0	<0.1	0.1	<0.1	–	–	–	–
Vibilia australis	–	–	–	–	3.3	0.2	0.1	<0.1
Vibilia viatrix	1.0	<0.1	0.1	<0.1	–	–	–	–
Unidentified Hyperiidea	14.8	0.2	0.8	0.5	23.3	0.7	0.9	0.9
Euphausiacea	(49.0)	(15.7)	(51.1)		(63.3)	(46.2)	(15.1)	
Euphausia pacifica	19.8	3.2	40.8	30.3	20.0	0.4	5.4	2.8
Thysanoessa spinifera	20.8	10.4	7.1	12.7	26.7	44.6	4.2	31.7
Unidentified furcilia	7.9	0.6	0.3	0.3	6.7	0.6	0.3	0.1
Unidentified remains	14.8	1.5	5.9	3.9	33.3	0.5	3.8	3.5
Decapoda	(22.5)	(12.5)	(1.3)		(25.0)	(4.9)	(4.6)	
Hippolytidae zoea	2.0	0.9	0.1	0.1	–	–	–	–
Natantia larvae	3.0	0.1	0.1	<0.1	3.3	<0.1	0.1	<0.1
Pagurus spp. megalopae	–	–	–	–	3.3	0.3	0.3	<0.1
Pugettia producta zoea	6.9	1.2	0.2	0.3	3.3	0.4	0.1	<0.1
Cancer antennarius meg.	1.0	0.6	<0.1	<0.1	3.3	<0.1	0.1	<0.1
Cancer magister meg.	1.0	<0.1	<0.1	<0.1	–	–	–	–
Cancer oregonensis meg.	5.9	3.7	0.3	0.8	–	–	–	–
Cancer spp. zoea	7.9	5.6	0.5	1.6	3.3	<0.1	0.1	<0.1
Pachycheles pubescens	–	–	–	–	3.3	1.1	1.0	0.2
Pachycheles rudis	–	–	–	–	3.3	1.0	0.1	<0.1
Porcellanid zoea	–	–	–	–	3.3	0.1	0.1	<0.1
Lophopanopeus bellus	–	–	–	–	3.3	0.1	0.1	<0.1
Pinnotherid megalopae	1.0	0.6	<0.1	<0.1	3.3	0.5	0.5	0.1
Hemigraspus oregonensis	–	–	–	–	3.3	1.1	0.5	0.1
Unidentified larvae	1.0	<0.1	<0.1	<0.1	10.0	0.2	0.4	0.1

Appendix Table 2 (continued)

Prey taxa	Chum salmon F	Chum salmon N	Chum salmon W	Chum salmon IRI	Sockeye salmon F	Sockeye salmon N	Sockeye salmon W	Sockeye salmon IRI
Arthropoda (continued)								
Crustacean remains	11.9	0.1	9.5	4.0	10.0	0.1	1.2	0.3
Insecta								
Diptera	1.0	<0.1	<0.1	<0.1	–	–	–	–
Unidentified	3.0	<0.1	<0.1	<0.1	–	–	–	–
Chaetognatha								
Sagita elegans	5.9	2.8	2.8	1.2	–	–	–	–
Unidentified	18.8	5.0	5.3	6.8	26.7	18.0	7.5	16.6
Chordata								
Larvacea								
Oikopleura sp.	2.0	2.4	0.4	0.2	–	–	–	–
Osteichthys	(30.4)	(15.0)	(10.4)		(56.7)	(16.2)	(58.2)	
Clupea harengus pallasi	–	–	–	–	3.3	0.2	3.1	0.3
Engraulis mordax	4.9	0.3	1.8	0.4	6.7	0.2	0.2	0.1
Osmeridae	2.0	0.6	0.6	0.1	20.0	1.1	29.0	14.7
Scorpaenichthys marmoratus	1.0	<0.1	<0.1	<0.1	–	–	–	–
Chitonotus pugetensis	1.0	0.3	0.1	<0.1	–	–	–	–
Cottidae	1.0	0.3	<0.1	<0.1	–	–	–	–
Ammodytes hexapterus	2.0	0.9	1.1	0.1	–	–	–	–
Ronquilus jordani	6.9	5.2	1.6	1.6	–	–	–	–
Unidentified larvae	7.9	3.2	1.3	1.2	16.7	14.1	9.3	9.5
Unidentified juveniles	1.0	1.4	0.3	1.0	–	–	–	–
Unidentified remains	10.9	2.9	2.1	1.9	13.3	0.5	11.3	3.8
Number of stomachs examined		109				32		
Number of empty stomachs		8				2		
Mean fork length (mm)		154.8				129.8		
Fork length range (mm)		97–237				104–149		

Spacing of Scale Circuli versus Growth Rate in Young Coho Salmon

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Abstract.–We compared rate of formation of scale circuli and spacing between circuli with fish growth rate and scale growth rate in three groups of young coho salmon *Oncorhynchus kisutch*): (1) smolts held in saltwater tanks, (2) tagged precocious males (jacks) returning to a release facility after only 3 or 4 months in the ocean in two different years, and (3) tagged juvenile coho salmon caught in the ocean. Rate of formation of scale circuli was significantly and positively correlated with fish growth rate and with scale growth rate in all groups. However, rate of circulus formation at a given growth rate was lower for large jacks than for the smaller and younger fish held in saltwater tanks, suggesting that rate of circulus formation is negatively related to size or age of fish as well as positively related to growth rate. Spacing of circuli was also significantly and positively correlated with fish growth rate in all but one group of returning jacks, and with scale growth rate in all groups. The relationship between circulus spacing and fish growth rate varied among groups, partly because the relationships between scale-radius and fish length and between rate of circulus formation and fish growth rate also varied among groups. Scale circulus spacing could be used to compare growth rates between groups of juvenile coho salmon that are of similar size and age and that have a common relationship between scale radius and fish length.

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Spacing of scale ridges (circuli) is a potentially valuable tool for comparing growth rates of fish where other data are not available. Scale circulus spacing has been found to be positively correlated with fish growth rate in several species of fishes (Doyle et al. 1987; Matricia et al. 1989; Glenn and Mathias 1985; Bhatia 1932; Bilton 1971a, 1975). Use of scales for studying growth has distinct advantages over other methods, such as the spacing of daily rings in otoliths, since scales can be easily obtained without killing the fish and are more quickly prepared and read.

Spacing of scale circuli is determined by both the rate at which circuli are formed and the rate of growth of the scale. Whether scale circulus spacing can be used to estimate fish growth rate depends on whether scale growth and circulus deposition rate are related to fish growth rate in a consistent, predictable manner. To determine the usefulness of circulus spacing for estimating growth rate of juvenile coho salmon, we investigated the relationships between scale radius and fish length, between rate of circulus formation and fish and scale growth rates, and between circulus spacing and fish and scale growth rates in three groups of marked young coho salmon: (1) subyearling (age 0) smolts held in saltwater tanks, (2) yearling (age 1.0)* fish returning as jacks to a coastal hatchery after 3 or 4 months in the ocean in two different years, and (3) marked juvenile coho salmon (age 0.0 and age 1.0) caught in the ocean within 2–4 months of entering the ocean. Our purpose was to develop a method for comparing growth rates of unmarked juvenile coho salmon caught in the ocean in different years (see Fisher and Pearcy 1988).

Methods

Coho smolts held in saltwater tanks

Coho smolts (age 0) were collected from one of the raceways at Oregon Aqua Foods, Inc's. Yaquina Bay, Oregon, release facility and transferred to the Hatfield Marine Science Center in July 1982. About 40 fish were placed in each of seven 1.5-m diameter fiberglass tanks. A constant flow of sea water was maintained to each tank. Daily food rations were varied between tanks from 0.6 to 3.0% of total salmon biomass in order to produce a wide range of fish growth rates. Fish in five tanks were fed Oregon Moist Pellet, while those in two others were fed thawed frozen euphausiids. Water temperature during the experiment was variable, ranging from approximately 11° to 17°C.

During 22–24 July, all the fish were anesthetized with MS-222, measured

* Age designation follows Koo (1962) and Godfrey et al. (1975), where the number to the left of the decimal indicates the number of winters spent in freshwater, and the number to the right of the decimal the number of winters spent in saltwater.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Fork length (FL, mm) vs. scale radius (SR, mm at 88×): Correlation coefficients (r) and geometric mean regressions (GM, Ricker 1973) for age-0 fish held in saltwater tanks (A), for age-1.0 jacks returning to Anadromous, Inc. in 1983 (B) and 1985 (C), and for juvenile coho (ages 0.0 and 1.0) caught in the ocean 1981–84 (D).

Group	n	r	GM regression
A	174	0.96	FL = 1.69 · (SR) + 18.54
B	64	0.78	FL = 1.59 · (SR) + 65.80
C	99	0.83	FL = 1.99 · (SR) + 43.05
D	34	0.96	FL = 2.13 · (SR) – 20.64

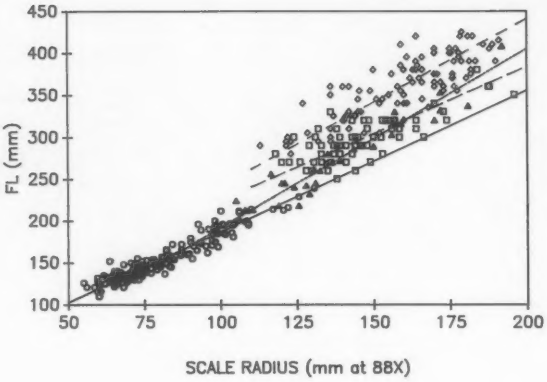

Figure 1

Fork length vs. scale radius scattergrams and GM regression lines for age-0 smolts held in saltwater tanks (○, ——), for age-1.0 CWT jacks returning to Coos Bay in 1983 (□, – –) and 1985 (◇, – –), and CWT juvenile fish caught in the ocean (▲, – · – ·).

to the nearest mm fork length (FL), and a scale sample taken from the preferred area (Clutter and Whitesel 1956). Each fish was also marked with a unique combination of color spots above the anal fin by injecting acrylic paint under the surface of the skin (Lotrich and Meridith 1974).

Fish were fed for 63–66 days. At the end of the period fish were again anesthetized, measured and weighed, and new scale samples were taken from the preferred area, although sometimes on the other side of the fish. Good scale samples were obtained from 80 fish at the beginning and end of the experiment. Mean fish lengths at the beginning and end of this 63–66 day period were 135 mm FL (SD 8.7, range 110–155 mm) and 171 mm FL (SD 24.5, range 125–229 mm), respectively. Acetate impressions were made of the scales. All scale measurements were made at a magnification of 88× along the axis 20° ventrad of the posterior-anterior axis of the scale.

Scales from each fish taken at the beginning and end of the experiment were compared to determine the spacing and number of circuli laid down during the intervening growth period. Mean circulus spacing during the growth period was calculated as $(SR_2 - SR_1)/n$, where SR_2 is the radius to last scale circulus, SR_1 is the radius to last circulus before the growth period as determined by comparison with the initial scale sample, and n is the number of new circuli formed during the growth period. Rate of circulus formation for each fish was also determined (n/d, where d is the duration of the experiment in days).

Linear growth rate was calculated for each fish as $(FL_2 - FL_1)/d$, where FL_1 and FL_2 are the lengths (mm) at the beginning and end of the experiment, respectively. Scale growth rate was also calculated as $(SR_{tot} - SR_1)/d$, where SR_{tot} is the total scale radius.

Returning Jacks

Fork length was measured and scale samples taken from the preferred area of 64 and 99 coded-wire tagged (CWT) jacks (precocious males) within 2 or 3 days of their return in 1983 and 1985, respectively, to the Anadromous Inc. facility on Coos Bay. Scales had also been taken earlier from a subsample of each release group shortly before their release as smolts. Fork length at time of ocean entrance was backcalculated for each returning jack using the relationship between scale radius and fork length at the time of release for that group and other groups released in the same month. (Tag groups were grouped by month of release to obtain adequate numbers for the prerelease scale radius-fish length relationships). Ocean entrance was detected on the scale as an abrupt change in circulus spacing (see Fisher and Pearcy, 1988). Since these fish were released and returned to a site only 8 km from the ocean, their period of growth in the ocean should be very similar to the time between their release and return. Growth rate of each fish while in the ocean was estimated by $(FL_2 - FL_1)/d$, where FL_2 is length on return to the hatchery, FL_1 is the backcalculated length at time of ocean entry, and d is the days between release and return. Scale growth rate was estimated as $(SR_{tot} - SR_1)/d$, where SR1 is the scale radius to the ocean entrance mark, and SR_{tot} is the total scale radius. Mean circulus spacing during the ocean growth period was calculated as the distance between the first and last ocean circulus divided by $n - 1$, where n = the number of circuli laid down during ocean growth.

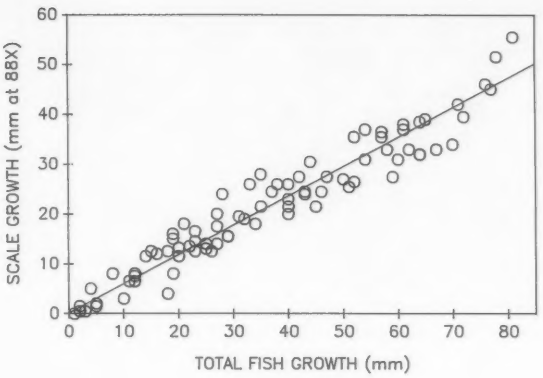

Figure 2
Scale growth vs. fish growth scattergram and GM regression line for individually marked age-0 smolts held in saltwater tanks.

Juvenile coho collected in the ocean

Growth rates in the ocean were estimated for CWT or spray-marked juvenile coho released (a) very near the ocean in Yaquina and Coos Bays and caught 60 or more days later in the ocean in August or September (15 fish), and (b) in the Columbia River (19 fish) and sampled during downstream migration near the ocean (at rkm 75, Dawley et al. 1985) and caught in the ocean 60 days or more after the median fish passed rkm 75, or released below rkm 75 and caught at least 60 days later in the ocean. For fish released in Yaquina or Coos Bays growth rate was estimated by $(FL_2 - FL_1)/d$ where FL_1 is the length at ocean entrance backcalculated from scales using a regression of FL on scale radius from a sample of fish taken at the time of release, FL_2 is length at capture in the ocean, and d is days between release and recapture. For Columbia River fish released in 1981, 1982, 1983, and 1984 length at ocean entrance was backcalculated using a regression of FL on scale radius derived from fish collected at rkm 75 in 1982 and 1983, combined. The number of days in the ocean was estimated from the date the median fish in each group passed rkm 75 and the mean downstream migration rates for each group. Estimated date of ocean entry for each group ranged from 3 to 11 days following passage of the median fish at rkm 75. For CWT Columbia River fish caught in 1984, when no sampling occurred at rkm 75, average downstream migration rates for tag groups from the same hatcheries in 1981–1983 were used in estimating ocean entrance date and days in the ocean (d). Scale growth rate for juvenile coho caught in the ocean was estimated the same way as for jacks.

Table 2
Rate of circulus formation (RCF, circuli per day) vs. fish growth rate (GR, mm/d): Correlation coefficients (r), probability that correlation = 0.0 (p), and geometric mean regression (GM) for age-0 fish held in saltwater tanks (A), CWT jacks (age 1.0) returning in 1983 (B) and 1985 (C), and CWT juvenile fish (both age 0.0 and 1.0) caught in the ocean (D).

Group	n	r	p	GM regression
A	80	0.89	<0.01	RCF = 0.18 · (GR) + 0.03
B	64	0.58	<0.01	RCF = 0.10 · (GR) + 0.03
C	99	0.57	<0.01	RCF = 0.10 · (GR) + 0.00
D	34	0.84	<0.01	RCF = 0.12 · (GR) + 0.02

Results

Fork length was positvely and significantly correlated with scale radius (SR) in all groups (Table 1, Fig. 1). The relationship (geometric mean regression, Ricker 1973) for each group of fish appeared linear. However, SR was smaller relative to FL for jacks returning in 1985 (diamonds in Figure 1) than for jacks returning in 1983 (squares) or for CWT juvenile coho salmon collected in the ocean (solid triangles). In addition, almost all FL–SR data points for returning yearling jacks and juveniles caught in the ocean were above the extrapolated regression line for the smaller subyearling fish held in saltwater tanks (Fig. 1). Thus, the relationships between FL and SR varied between age or size groups (small subyearling fish vs. larger yearling jacks and juveniles caught in the ocean) and between years (1983 vs. 1985 Anadromous Inc. jacks). The relationship between scale growth and fish growth appeared linear for the subyearling coho smolts held in saltwater tanks (Fig. 2).

Rate of circulus formation was positively and significantly ($r = 0.57 - 0.89$, $p<0.01$) correlated with fish growth rate for all groups (Table 2, Fig. 3). However the slope of the relationship was lower for ocean-caught juveniles and jacks returning in 1983 and 1985 (slopes of GM regression = 0.12, 0.10, 0.10, respectively) than for the subyearling fish held in saltwater tanks (slope = 0.17) At similar fish growth rates, rates of circulus formation were generally higher for the subyearling fish held in saltwater tanks than for juveniles caught in the ocean or for returning jacks (Fig. 3).

The spacing between circuli was positively and significantly correlated with fish growth rate for all groups but jacks returning in 1983 (Table 3). The correlation was strong ($r = 0.80$) for age 0.0 fish held in saltwater tanks, but much weaker for jacks returning in 1985 ($r = 0.24$). However, the relationship between circulus spacing and fish growth rate for subyearling

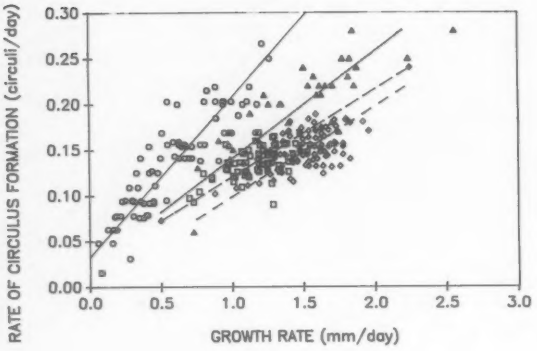

Figure 3

Rate of circulus formation vs. fish growth rate scattergrams and GM regression lines for age-0 smolts held in saltwater tanks (○, —), for CWT jacks returning to Coos Bay in 1983 (□, — —) and 1985 (◇, – –), and for CWT juvenile fish caught in the ocean (▲, – · · –).

Table 3

Circulus spacing (CSP, mm at 88×) vs. fish growth rate (GR, mm/d): Correlation coefficients (r), probability that correlation coefficient = 0.0 (p) and geometric mean regression (GM) for age-0 fish held in saltwater tanks (A), CWT jacks (age 1.0) returning in 1983 (B) and 1985 (C), and CWT juvenile fish (both ages 0.0 and 1.0) caught in the ocean (D).

Group	n	r	p	GM regression
A*	80	0.80	<0.01	CSP = 1.80 · (GR) + 1.31
B	64	0.08	N.S.	—
C	99	0.24	<0.05	CSP = 2.06 · (GR) + 0.71
D	34	0.52	<0.01	CSP = 1.21 · (GR) + 2.24

*For this group of fish the correlation coefficient for a third-order relationship, $CSP = 0.91 + 5.35(GR) - 6.44(GR)^2 + 3.04(GR)^3$, $r = 0.83$, was higher than for the linear relationship.

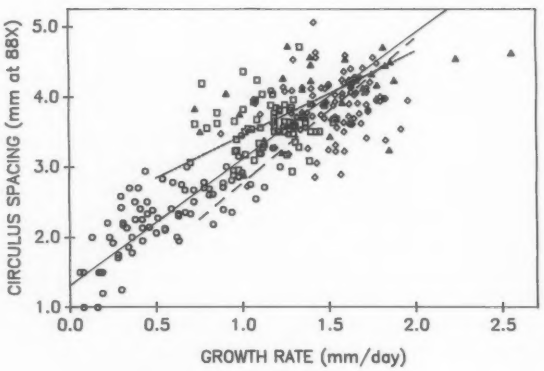

Figure 4

Circulus spacing vs. growth rate scattergrams and GM regression lines for age-0 smolts held in saltwater tanks (○, —), for CWT jacks returning to Coos Bay in 1983 (□, regression n.s.) and 1985 (◇, – –) and for CWT fish caught in the ocean (▲, – · · –).

fish held in saltwater tanks appeared to be nonlinear (see footnote, Table 3). In general, circulus spacing vs. growth rate values in the three groups that had reared in the ocean were fairly close to the extrapolated linear regression line for the smaller fish held in saltwater tanks, although the variability about this regression line was very large (Fig. 4). Mean growth rates of jacks returning in 1985 and juveniles caught in the ocean (1.49 mm/d and 1.53 mm/d, respectively) were significantly greater (t-tests, $p<0.01$) than the mean growth rate of jacks returning in 1983 (1.17 mm/d). Mean circulus spacings of the two faster growing groups (3.86 and 4.04 mm at 88× for jacks returning in 1985 and for juveniles caught in the ocean, respectively) were also both greater ($p<0.01$) than mean circulus spacing of the slower-growing jacks returning in 1983 (3.61).

In each group of fish some of the large variability in the relationship between circulus spacing or circulus deposition rate and fish growth rate was caused by variability in the relationship between fish length and scale radius. To remove this component of variation, we compared circulus spacing and circulus deposition rates with scale growth rates (Tables 4 and 5, respectively). Correlation coefficients for the relationships of circulus spacing and deposition rate with scale growth rate were considerably higher than for the corresponding relationships with fish growth rate, especially for jacks returning to Coos Bay in 1983 and 1985. (Compare Tables 2 with 4, and 3 with 5.) Circulus spacing was positively and significantly correlated with scale growth rate in all groups, whereas the relationship between circulus spacing and fish growth rate was significant for all groups but jacks returning in 1983. Thus, the correlations of circulus spacing or rate of circulus formation with scale growth rate were stronger than the correlations with the underlying fish growth rate.

Discussion

A positive correlation between rate of circulus formation and fish growth rate appears to be a common feature among fishes. We found in young coho salmon that rate of circulus deposition was positively and

Table 4

Rate of circulus formation (RCF, circuli/d) vs. scale growth rate (SGR, mm/d at 88×): Correlation coefficients (r), probability that correlation coefficient = 0.0 (p) and geometric mean regression (GM) for age-0 fish held in saltwater tanks (A),CWT jacks (age 1.0) returning in 1983 (B) and 1985 (C), and CWT juvenile fish (both age 0.0 and 1.0) caught in the ocean (D).

Group	n	r	p	GM regression
A	80	0.94	<0.01	RCF = 0.30(SGR) + 0.03
B	64	0.84	<0.01	RCF = 0.22(SGR) + 0.03
C	99	0.83	<0.01	RCF = 0.20(SGR) + 0.03
D	34	0.90	<0.01	RCF = 0.22(SGR) + 0.02

Table 5

Circulus spacing (CSP, mm at 88×) vs. scale growth rate (SGR, mm/d at 88×): Correlation coefficients (r), probability of correlation coefficient = 0.0 (p) and geometric mean regression (GM) for age-0 fish held in saltwater tanks (A), CWT jacks (age 1.0) returning in 1983 (B) and 1985 (C), and CWT juvenile fish (both age 0.0 and 1.0) caught in the ocean (D).

Group	n	r	p	GM regression
A*	80	0.82	<0.01	CSP = 3.07(SGR) + 1.29
B	64	0.62	<0.01	CSP = 4.22(SGR) + 1.39
C	99	0.59	<0.01	CSP = 4.14(SGR) + 1.56
D	34	0.56	<0.01	CSP = 2.26(SGR) + 2.22

*For this group of fish the correlation coefficient for a third order relationship, $CSP = 1.02 + 6.92(SGR) - 10.37(SGR)^2 + 6.77(SGR)^3$, $r = 0.84$, was higher than for the linear relationship.

significantly correlated with scale and fish growth rates (Tables 2, 5; Fig. 3). Thus, the faster the fish or scales grew, the more circuli were formed per unit time. Positive correlations between rate of circulus formation and growth rate also have been found for walleye (Glenn and Mathias 1985) and cichlids (Sire 1986). In juvenile walleye, rate of circulus formation ranged from 1.5 circuli/d at high growth rates to 1 circulus every 2–3 weeks at low growth rates. Data presented by Bilton and Robins (1971a) indicated that juvenile sockeye salmon receiving more food, and presumably growing faster, produced more circuli during a given period than those fish that were fed less. Bilton and Robins (1971b) also found that sockeye salmon formed no circuli during periods of starvation. In chum salmon from Olsen Creek, Alaska, the number of circuli and radius to the middle of the first ocean annulus were positively correlated (Helle 1980). Therefore, if time to the middle of the first ocean annulus was constant (which may or may not be true), then fast-growing fish (larger radius) produced more circuli per unit time than slow-growing fish.

Positive correlations between circulus spacing and growth rate also have been reported in other species of fish. Bhatia (1932) found that scales from juvenile rainbow trout fed abundantly and growing rapidly, and scales from those fed sparsely and growing slowly had zones of widely spaced and narrowly spaced circuli, respectively, near the scale margin. Bhatia also was able to produce zones of widely and narrowly spaced circuli by alternately changing feeding level. Doyle et al. (1987) and Matricia et al. (1989) found positive correlations between circulus spacing and fish growth rate in tilapia. Sire (1986) found more widely spaced circuli among faster growing than slower growing cichlids. In juvenile walleye, mean spacing of circuli formed during the period of most rapid growth was found to be greater than mean spacing of circuli formed during periods of slower growth (Glenn and Mathias 1985). Bilton and Robins (1971a) found a significant positive correlation between feeding level and spacing of circuli in sockeye salmon.

Rate of circulus formation and spacing of circuli are probably related to a number of other factors beside growth rate. We found that rate of circulus formation for juvenile coho salmon caught in the ocean and especially for returning jacks were all well below the rates predicted by the regression for the much smaller fish held in saltwater tanks but growing at similar rates (Fig. 3). This suggests that the rate of circulus formation varies with age or size of fish or with environmental conditions, as well as with growth rate. Doyle et al. (1987) found that circuli of tilapia were laid down less frequently as fish grew larger. They also found that the relationship between growth rate and circulus spacing was stronger when a correction was made for the size of fish. Bilton (1975) suggested that rate of circulus deposition was probably a function of a combination of factors such as temperature, food, light, and maternal and inherent characteristics.

Several studies have addressed the possible effects of water temperature on circulus spacing. Generally they suggest that the effect of temperature, by itself, on circulus spacing is relatively small compared with the effect of feeding level or growth rate. By manipulating feeding level, Bhatia (1932) was able to produce zones of widely and narrowly spaced circuli in scales of rainbow trout growing in extremely different water temperatures (4°C and 17°C). Kimura and Sakagawa (1972), working with sardines, found that formation of annuli or checks (bands of narrowly spaced circuli) did not appear to be related to temperature. Barber and Walker (1988) found that in sockeye salmon annulus formation occurred before the coldest months of the

year and that during the coldest months widely spaced circuli were formed. Hogman (1968) cited work by Deason and Hile (1947) that indicated that annuli and checks formed in scales of kiyis living at depth in Lake Michigan, despite a very small annual variation in water temperature (2–3°C). Bhatia (1932) cited his earlier work showing that when rainbow trout were fed uniformly throughout the year no periodic zones were formed on their scales and all rings were of nearly the same width despite fluctuations in temperature. However, there is some evidence that in brown trout water temperature during egg and alevin stages prior to scale formation affected subsequent rate of circulus formation (Skurdal and Anderson 1985).

Inherent differences between groups of fish may mask the relationship between circulus spacing and growth rate. For example, for coho jacks returning to the Anadromous Inc. facility in Coos Bay in 1985, scales were generally smaller at a given fish length (Fig. 1), and rate of circulus formation was lower at a given growth rate (Fig. 2), than was the case for CWT juveniles caught in the ocean. This resulted in significantly different mean spacing of circuli in these two groups (3.86 vs. 4.04, t-test, $p<0.05$) despite very similar mean growth rates (1.53 and 1.49 mm/d, t-test, n.s.). Because of differences in the relationships between circulus spacing and growth rate among different groups of juvenile coho salmon, inferences about relative growth rates based on scale circulus spacing are probably only valid when made between groups that are similar in age, size, and morphometric characteristics (i.e., very similar SR–FL relationships).

Data from the group of subyearling fish held in saltwater tanks suggest that the relationship between circulus spacing and growth rate may be complicated. A third-order relationship (see footnote, Table 3) gave a better fit to the data than did a simple linear relationship. In this group of fish there was little change in circulus spacing between growth rates of 0.4 and 0.9 mm/d. More rapid changes in circulus spacing with growth rate occurred both above and below this range (circles, Fig. 4). This result suggests that for coho salmon there may be ranges of growth rates within which circulus spacing is a poor indicator of relative growth rate.

We compared mean circulus spacing in the ocean growth zone of scales for unmarked yearling (age 1.0) juvenile coho caught in the ocean in late summer of 1981, 1982, 1983, and 1984 (Fisher and Pearcy 1988). These fish had very similar SR–FL relationships in all years and were of similar size at time of entry into the ocean (based on backcalculated size at ocean entry). We also estimated growth rates of these unmarked juvenile yearling coho salmon between early and late summer (between June and August or September) from changes in mean lengths with time (see Fisher and Pearcy 1988, their Table 3). Rank order of mean spacing between circuli and growth rates estimated from shifts in mean FL with time are compared in Table 6. Although the rank orders do not agree in detail, they both suggest higher fish growth rates during the summers of 1981 and 1982 than in 1983 and 1984.

Table 6

Rank order of mean scale circulus spacing for unmarked juvenile coho collected in the ocean during the late summer, 1981–84, and growth rates of unmarked juvenile coho estimated from changes in mean length between early and late summer (see Fisher and Pearcy 1988, their Tables 3 and 4).

Year	Mean spacing (mm at 88×)	Rank	Est. growth rate (mm/d)	Rank
1981	4.16	1	1.56	2
1982	4.15	2	1.76	1
1983	3.91	4	1.37	3
1984	3.95	3	1.33	4

Acknowledgments

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Multispecies Harvesting Policies for Washington-Oregon-California Rockfish Trawl Fisheries

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Abstract.—Optimal harvesting policies were developed for a model of the Washington-Oregon-California trawl fisheries for bocaccio *Sebastes paucispinus*, chilipepper *S. goodei*, widow rockfish *S. entomelas*, splitnose rockfish *S. diploproa*, and shortbelly rockfish *S. jordani*. In the simulated management system, the annual quota for each species was based on an intended fishing mortality rate (F) and an estimate of stock biomass. Traditional constant F policies were compared with variable F policies in which F was a linear function of either stock biomass (single-species) or the combined biomass of all other species (multispecies). Variable F policies were ineffective for increasing total harvest of all species combined, when compared with constant F policies. However, both single-species and multispecies variable F policies were found to reduce the variance for total harvest substantially with no significant loss in yield. The reduction in variance was roughly equal to the reduction that would be achieved by lowering the coefficient of variation (CV) for biomass estimates from 50% to 25% or from 25% to 0%. The reduction in variance generally was greater for the multispecies than for the single-species variable F policy. Compared with the case where CV = 0%, average total yield was reduced slightly for both constant F and variable F policies when CVs for biomass estimates were greater than 0%.

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In the Washington-Oregon-California (WOC) trawl fisheries for rockfish (*Sebastes* spp.), the landings are comprised of many species, including bocaccio *S. paucispinus*, chilipepper *S. goodei*, Pacific ocean perch *S. alutus*, canary rockfish *S. pinninger*, widow rockfish *S. entomelas*, and yellowtail rockfish *S. flavidus* (PFMC 1982). There is little evidence of substantial biological interaction among the adults of these species. Technological interactions (Pope 1979) are significant in the shelf rockfish fishery (Pikitch 1987), which accounts for most of the landings of bocaccio, chilipepper, and canary and yellowtail rockfish. Fishermen have some control over the species composition of the catch in this fishery by varying the areas or depths fished. The other significant rockfish fishery is the midwater trawl fishery for widow rockfish. Catches of other rockfish species are negligible in that fishery.

Most currently marketed *Sebastes* species have similar or equal value to fishermen; consequently, fishermen are more concerned about the aggregate yield than about the species composition of the catch. Thus, it seems reasonable to ask whether efforts to vary the annual proportions harvested for these species would result in benefits to the resource or to the fishing industry. For example, reducing the variability of annual quotas has been an important concern for the west coast fishing industry. The objective of this study was to evaluate multispecies harvesting policies for the WOC trawl fisheries for rockfish to determine whether total yield (all species combined) can be increased or the variance for total yield can be reduced. Specifically, I compared the performance of policies obtained using (1) risk-neutral and risk-averse objective functions, (2) constant and variable fishing mortality rates (F), and (3) abundance estimates for a single species or multiple species.

Except for widow rockfish, relatively little is known about the population dynamics of these stocks. For that reason, this study should be viewed as an exploratory analysis of alternative harvesting policies, and not as a basis for regulatory changes by the Pacific Fishery Management Council. It may be worthwhile to develop similar harvesting policies for Council review once we have adequate life-history information about the commercially important groundfish stocks. The harvesting policies examined in this study should be useful in other cases where fishermen derive income from several species and have some control over the species composition of the catch.

Methods

This section provides an overview of the model structure, harvesting policies, and life-history data. A detailed description of methods is provided elsewhere (Hightower 1990).

I developed optimal harvesting policies for two-, three-, and five-

species models in order to evaluate changes in policy performance as additional species were included. The selected species (bocaccio, chilipepper, widow rockfish, splitnose rockfish *S. diploproa*, and shortbelly rockfish *S. jordani*) all occur off California, support or could support significant commercial fisheries, and have a wide range of life-history types. I used bocaccio and chilipepper for the two-species model because they were estimated to have similar biomass levels. I included widow rockfish for the three-species model because it was estimated to have about twice the maximum sustainable yield level of biomass of bocaccio and chilipepper. For the five-species model, shortbelly and splitnose rockfish were added as examples of relatively short- and long-lived rockfish species, respectively. Shortbelly rockfish biomass also is substantially higher than that of the other four species.

Model structure

I used Schnute's (1985) generalization (eq. 2.7) of Deriso's (1980) delay-difference model to represent the dynamics of each stock:

$$B_t = (1+\rho)S_{t-1}B_{t-1} - \rho S_{t-1}S_{t-2}B_{t-2} + R_t - \rho(v/V)S_{t-1}R_{t-1} \quad (1)$$

where B_t was the fishable population biomass at the beginning of year t; S_t was the survival rate in year t; ρ, v, and V were parameters for the growth curve; and R_t was the recruitment biomass at the beginning of year t. Growth parameters ρ, v, and V were estimated by fitting the following curve relating mean weight at age a (w_a) to age:

$$w_a = v + (V-v)(1-\rho^{1+a-k})/(1-\rho) \quad (2)$$

where V and v were parameters representing mean weight at the age of recruitment (age k) and at age k−1, respectively, and ρ was a parameter describing the growth rate (Schnute 1985, eq. 1.14). Following Kimura et al. (1984), I assumed that B_0 (needed to calculate B_2) equaled the starting biomass level B_1.

Recruitment was calculated from a Beverton-Holt stock-recruitment curve (Kimura 1988):

$$R_{t+k} = R_\infty(B_t/B_\infty)/(1 - A(1 - B_t/B_\infty))\exp(z_t) \quad (3)$$

where R_∞ was the virgin recruitment level associated with virgin stock biomass B_∞, A was the level of density-dependence assumed in the stock-recruitment relationship, and $\exp(z_t)$ was the lognormal error term used to introduce random variability in recruitment. Estimates of A were not available for any of the stocks used in this study. To introduce a degree of density-dependence into the model, I assumed arbitrarily that recruitment decreased by 10% when spawning stock decreased by 50%. That assumption has been used in earlier stock-assessment studies (Lenarz 1984, Henry 1986, Methot and Hightower 1988, Tagart 1988) to obtain harvest recommendations assumed to be conservative when information on the stock-recruitment relationship was unavailable. The normal random variate z_t was assumed to have mean 0 and variance σ^2. I assumed that $R_1 \ldots R_k$ were produced by a stock equal in size to B_1 because the actual B values producing those year-classes were not known.

Harvesting policies

In the harvesting policies used in this study, the annual fishing mortality rate for species j in year t ($F_j[t]$) was either a constant

$$F_j[t] = b_{j,0} \quad \text{(constant F)}, \quad (4)$$

a function of stock biomass

$$F_j[t] = b_{j,0} + b_{j,1} B_j[t] / B_{\infty,j} \quad \text{(variable F)}, \quad (5)$$

or a function of the combined biomass of all other stocks

$$F_j[t] = b_{j,0} + b_{j,1} \sum_{i \neq j} B_i[t] / \sum_{i \neq j} B_{\infty,i}, \quad \text{(multispp. var. F)} \quad (6)$$

Policies (5) and (6) were similar in form to a linear model Hilborn (1985) used to calculate catch as a function of stock biomass. Biomass estimates were scaled by virgin biomass so that the policy parameters were relatively independent of absolute biomass levels. Estimates of the policy parameters ($b_{j,0}$, $b_{j,1}$; j=1,..,s species in model) were obtained using stochastic approximation (Ruppert et al. 1984).

Objective functions

As in earlier optimization studies (Ruppert et al. 1984, Hilborn 1985), I obtained policies for maximizing total catch

$$\max \sum_t C[t], \text{ where } C[t] = \sum_j C_j[t]$$

(maxh objective function)

and the natural logarithm of total catch

$$\max \sum_t \log(C[t]) \qquad \text{(logh objective function).}$$

For most of the WOC trawl fisheries, the goal of the Pacific Fishery Management Council is to maximize long-term average yield by maintaining F at a specified level. Thus the maxh objective function corresponds to the current approach to management. Relative to maxh policies, logh policies tend to provide less variable catches so they may be more appropriate in fisheries where price is sensitive to volume, the fishery provides a substantial fraction of a fisherman's annual income, or stability of volume is critical for marketing reasons (Deriso 1985). Mendelssohn (1982) and Ruppert et al. (1985) used maxh and logh policies to represent extremes along a risk continuum, in that maxh policies are risk-neutral (marginal utility does not change with increasing catch) and logh policies are risk-averse (marginal utility decreases with increasing catch).

I also evaluated a third more conservative objective function for maximizing an exponential function of total catch:

$$\max \sum_t (1 - \exp(-C[t]/\delta)) \quad \text{(negx objective function)}$$

where δ was a scaling factor (Raiffa 1968). At small values of δ (relative to C[t]), the marginal utility of additional units of catch decreases rapidly. If δ is large, utility increases linearly with increasing catch. In order to obtain highly risk-averse policies, I used $\delta = 5$ for C[t] values of about 5 (2-species case) to 30 (5-species case). Using this δ value, negx policies were even more conservative than logh policies (Fig. 1). Of course, other objective functions (and harvesting policies) could be chosen that would provide greater reductions in the variance of catch. For example, Murawski and Idoine (1989) compared a series of constant-catch harvesting policies for Georges Bank haddock *Melanogrammus aeglefinus*. For a sufficiently low target catch (45% of the average catch under a constant $F = F_{0.1}$ policy), year-to-year variability in catch was zero. The logh and negx objective functions used in this study were intended to provide a compromise between maximizing catch and minimizing variability of catch.

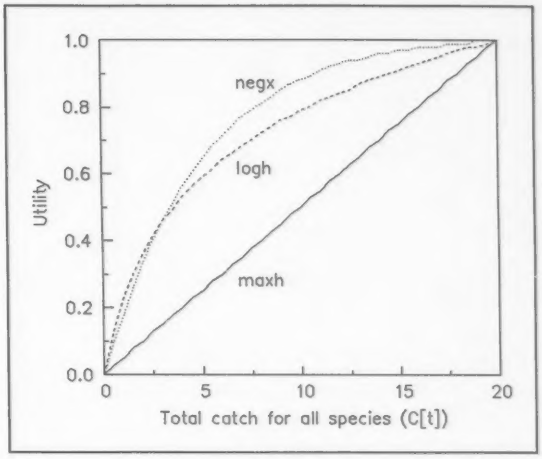

Figure 1

Alternative measures of the utility of the total rockfish catch in year t (C[t]), as determined by objective functions maxh:Utility(C[t]) = C[t], logh:Utility(C[t]) = $\log_e$(C[t]), and negx:Utility(C[t]) = 1 − exp(−C[t]/5). Utilities for each objective function were scaled to a maximum value of 1.

Planning horizon

The optimization studies were done using a 100-year planning horizon in order to obtain steady-state harvesting policies. In the two- and three-species cases, the bocaccio, chilipepper, and widow rockfish stocks declined to varying degrees at the start of the planning horizon but reached steady-state levels by about year 50 (Fig. 2). In the five-species case, sharp initial declines were noted for the unexploited splitnose and shortbelly rockfish stocks. Because of its long life-span and slow growth-rate, the splitnose rockfish stock continued to decline throughout the planning horizon. Based on a series of optimization runs, I found that the constant F for splitnose rockfish that maximized mean harvest decreased as the horizon length increased for policies up to 200 years in length. Planning horizons greater than 100 years were impractical, however, due to computing costs. Therefore, in order to obtain results that were not dependent on the length of the planning horizon, I obtained policies for the five-species model using a 75-year transient phase within a 100-year horizon (Law and Kelton 1982). Using this approach, the objective function was based only on harvests in years 75–100. Steady-state biomass levels were reached within 100 years for all species except possibly splitnose rockfish; thus, declines in stock size at the start of the planning horizon were due only to high initial biomass levels (Fig. 3).

Errors in biomass estimates

Most of the harvesting policies evaluated in this study required biomass estimates for one or more species in order to calculate the policy Fs used to determine the annual quotas. To evaluate the practicality of these policies, I introduced a random error term so that the harvesting policy and resultant catch quota in year t were based on simulated estimates $B'_1[t] \ldots B'_s[t]$ of

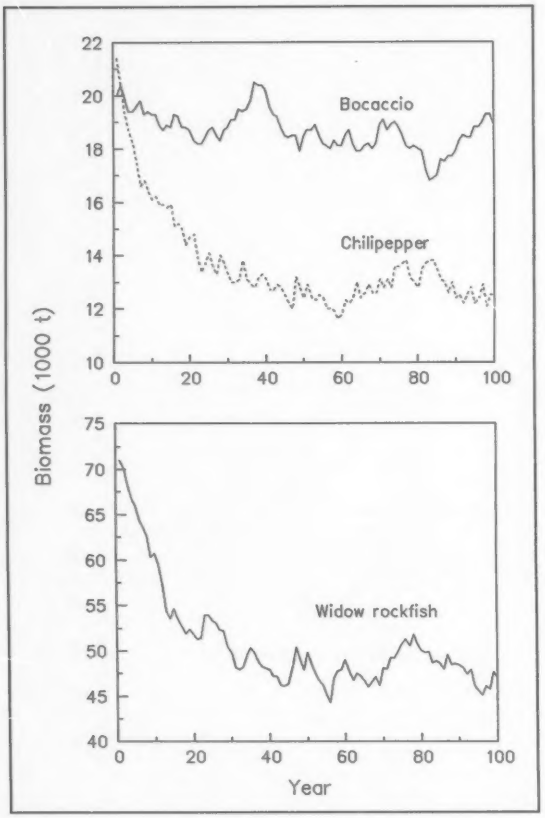

Figure 2

Mean rockfish biomass from 100 replicate 100-year simulation runs for the three-species model, using the constant fishing mortality rates that maximized harvest and assuming that the coefficient of variation for biomass estimates was 0. Results for the two-species model with only bocaccio and chilipepper were similar and are not shown here.

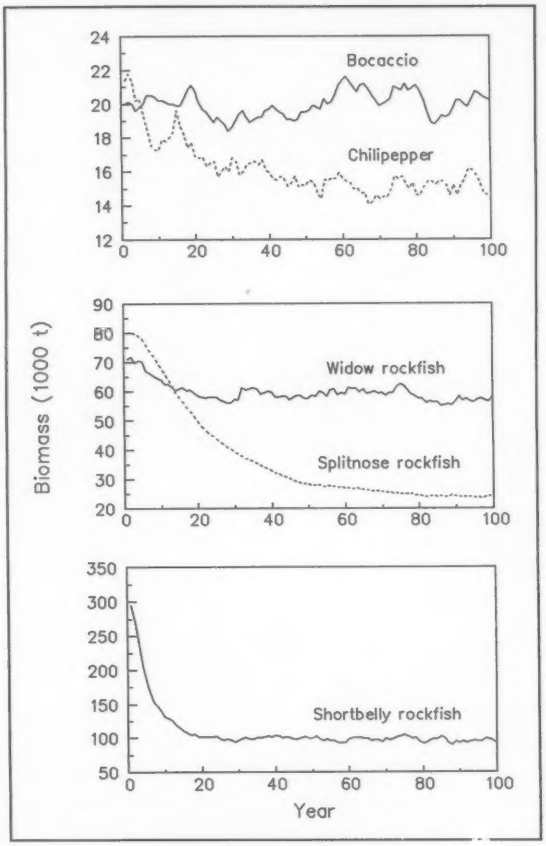

Figure 3

Mean rockfish biomass from 100 replicate 100-year simulation runs for the five-species model, using the constant fishing mortality rates that maximized harvest and assuming that the coefficient of variation for biomass estimates was 0.

the actual biomass levels $B_1[t]..B_s[t]$. Following an assumption made by Pope and Gray (1983) regarding data used in stock assessments, I assumed that errors in biomass estimates were lognormally distributed and independent over time. The coefficient of variation (CV) for biomass estimates was either 0, 25, or 50%, based on a review of the stock-assessment literature (Rivard 1981, Pope 1983, Pope and Gray 1983, Sen 1984, Weinberg et al. 1984, Methot 1986).

Because the WOC trawl fisheries for rockfish are regulated through catch quotas, F′ (the policy F based on estimates $B'_1[t]..B'_s[t]$) was used to calculate the annual quota $C_j[t]$ as $B'_j[t]F'_j[t](1 - \exp(-M_j - F'_j[t])/Z'_j[t]$. $B_{\infty,i}$ (the virgin biomass level used in the variable F policies) and M_j were assumed to be known without error. The actual F required to obtain $C_j[t]$ from $B_j[t]$ ($F_j[t]$) was either higher or lower than the intended F ($F'_j[t]$), depending on the direction and magnitude of errors in $B'_1[t]..B'_s[t]$.

Life-history information

The reliability of the parameter estimates (Table 1) varies, depending on the length and magnitude of the historical fishery for each species. A significant fishery for widow rockfish developed in 1979, with average 1980–85 landings of 17200 t (Hightower and Lenarz 1986). Fisheries for bocaccio and chilipepper have existed for decades; average 1980–85 landings were 3200 t for bocaccio and 1700 t for chilipepper (PFMC 1986). Preliminary stock assessments based on catch-at-age data have been completed for all three species. Land-

Table 1

Parameters used in delay-difference models for each rockfish species. Methods used to estimate the life-history parameters are described in detail by Hightower (1990).

	widow	bocaccio	chilipepper	splitnose	shortbelly
k	6	4	8	12	4
v (kg)	0.436	0.061	0.581	0.327	0.078
V (kg)	0.598	0.553	0.796	0.343	0.110
ρ	0.903	0.933	0.878	0.984	0.825
M	0.15	0.25	0.20	0.05	0.20
B_∞ (t)	180.0	60.0	47.7	80.0	295.0
B[1] (t)	71.0	20.0	21.4	80.0	295.0

Table 2

Fishing mortality rates of rockfish obtained for constant F policies maximizing harvest (maxh), log(harvest) (logh), or a negative exponential function of harvest (negx) for two-, three-, and five-species models.

Species	Objective function	Fishing mortality rate				
		bocaccio	chilipepper	widow	splitnose	shortbelly
Two	maxh	0.200	0.269	—	—	—
	logh	0.195	0.255	—	—	—
	negx	0.194	0.250	—	—	—
Three	maxh	0.201	0.264	0.181	—	—
	logh	0.196	0.254	0.174	—	—
	negx	0.191	0.242	0.163	—	—
Five	maxh	0.182	0.222	0.153	0.056	0.229
	logh	0.181	0.218	0.152	0.055	0.224
	negx	0.187	0.211	0.146	0.055	0.204

ings of splitnose and shortbelly rockfish have been negligible to date; consequently, parameter estimates for those species should be viewed as highly preliminary.

Results and discussion

Objective functions

Results were similar for constant F policies using different objective functions. Optimal constant Fs generally were comparable with M, although the F for chilipepper (M = 0.20) was higher than that for bocaccio (M = 0.25) (Table 2). That apparently was due to the higher age at first recruitment for chilipepper. (For bocaccio and chilipepper, the slight differences in constant Fs in the two- and three-species cases were due to random error.) Optimal Fs were lower for the five-species case than for the two- and three-species cases because harvests in years 1–74 were excluded from the five-species objective function. Policies obtained assuming a transient period may be unacceptable on socio-economic grounds but can probably be viewed as a practical lower bound for F.

For each of the models, the differences in F, total yield, and variance for total yield showed a consistent trend: highest for maxh policies, intermediate for logh policies, and lowest for negx policies (Tables 2–5). Relative to the variance for maxh policies, logh constant F policies resulted in about a 2% reduction in total variance, whereas variances for the negx policies were 3 (2-species case) to 10% (5-species case) lower. These results illustrate that moderately lower variances can be achieved by using slightly lower Fs and accepting slightly lower total yields.

Constant vs. variable F policies

The variable F policies (5)–(6) for maximizing harvest did not increase total yield significantly compared to the constant F policies (Tables 3–5). Results from earlier studies suggest that the degree of increase due to a variable F policy may depend on the assumed life-history characteristics. For example, a 17% increase

Table 3

Comparison of average rockfish catches and year-100 variances for constant F, single-species variable F, and multispecies harvesting policies. CVs for biomass estimates were assumed to be 0%.

			Mean yield						Var[100]					
Species	Harvesting policy	Objective function	bocaccio	chili-pepper	widow	split-nose	short-belly	total	bocaccio	chili-pepper	widow	split-nose	short-belly	total
Two	const F	maxh	3.02	2.96	—	—	—	5.98	0.97	1.46	—	—	—	2.87
		logh	3.02	2.96	—	—	—	5.98	0.96	1.42	—	—	—	2.81
		negx	3.02	2.95	—	—	—	5.97	0.95	1.40	—	—	—	2.78
	variable F	maxh	3.05	3.02	—	—	—	6.05	1.49	3.81	—	—	—	6.00
		logh	3.03	2.96	—	—	—	5.96	0.91	1.17	—	—	—	2.44
		negx	3.02	2.95	—	—	—	5.95	0.84	1.09	—	—	—	2.27
	multispp.	maxh	3.02	2.96	—	—	—	5.98	0.95	1.48	—	—	—	2.83
		logh	3.00	2.95	—	—	—	5.95	0.92	1.36	—	—	—	1.94
		negx	2.99	2.94	—	—	—	5.93	0.95	1.32	—	—	—	1.70
Three	const F	maxh	3.02	2.95	7.78	—	—	13.75	1.01	1.28	4.92	—	—	7.40
		logh	3.04	2.94	7.77	—	—	13.75	1.01	1.26	4.85	—	—	7.29
		negx	3.03	2.93	7.75	—	—	13.71	1.00	1.23	4.72	—	—	7.12
	variable F	maxh	3.06	3.01	7.92	—	—	13.93	1.47	3.08	14.12	—	—	18.55
		logh	3.05	2.97	7.82	—	—	13.78	1.18	1.34	4.86	—	—	7.59
		negx	3.03	2.93	7.70	—	—	13.61	0.93	1.04	3.72	—	—	5.75
	multispp.	maxh	3.03	2.94	7.77	—	—	13.74	1.01	1.28	4.96	—	—	7.74
		logh	3.02	2.94	7.75	—	—	13.70	1.02	1.26	4.68	—	—	5.60
		negx	2.98	2.91	7.70	—	—	13.60	1.06	1.20	4.36	—	—	4.08
Five	const F	maxh	3.04	2.85	7.82	1.97	19.92	35.59	1.13	0.74	5.90	0.08	69.56	78.05
		logh	3.05	2.86	7.84	1.94	19.93	35.48	1.13	0.73	5.86	0.08	67.97	76.42
		negx	3.05	2.85	7.82	1.94	19.58	35.09	1.14	0.72	5.73	0.08	61.90	70.19
	variable F	maxh	3.06	2.90	7.95	2.30	20.84	36.91	1.53	1.22	16.96	0.21	431.37	460.41
		logh	3.06	2.89	7.91	2.43	20.02	36.17	1.40	0.84	7.56	0.25	70.84	82.13
		negx	3.03	2.85	7.70	1.49	18.58	33.53	0.99	0.70	3.70	0.20	26.41	32.10
	multispp.	maxh	3.03	2.87	7.85	1.99	20.07	35.67	1.18	0.74	5.90	0.08	70.92	78.16
		logh	2.89	2.58	7.52	1.37	19.61	33.83	1.28	0.93	6.01	0.63	68.64	44.60
		negx	2.46	2.64	7.72	1.41	19.37	33.46	1.64	0.69	5.52	0.20	59.66	43.70

in yield was reported for Atlantic menhaden *Brevoortia tyrannus* (Ruppert et al. 1985), compared with only 1–2% for Pacific whiting *Merluccius productus* (Swartzman et al. 1983) and widow rockfish (Hightower and Lenarz 1989). Because, in this study, there was no apparent advantage in using variable F policies to maximize harvest, the remaining results and discussion focus on a comparison of the traditional constant F policy for maximizing harvest versus variable F policies (5) and (6) for the logh and negx objective functions.

Compared with a constant F policy, variable F policies (5) and (6) provided a substantial reduction in the variance of total yield with only a negligible loss in yield. (The reductions in variance would be slightly less if constant F and variable F policies for the same objective function were compared.) The reduction in variance did not appear to be particularly sensitive to the number of species included, their life-history characteristics, or the degree of correlation among species for recruitment perturbations (Hightower 1990). However, the level of density-dependence in the stock-recruitment relationship may affect the relative performance of different harvesting policies. In limited additional runs, I found that the difference between constant F and variable F policies generally decreased as the degree of density-dependence increased (i.e., as stock-recruitment parameter A decreased). When recruitment declined markedly with reductions in spawning stock, both types of harvesting policies were necessarily quite conservative.

The advantage of the variable F policies can be illustrated by examining a Pareto Frontier (Walters 1975), which shows the relationship between mean catch and its variance. I developed frontiers for the two-, three-, and five-species cases by simulating the fishery at 20, 40, 60, 80, and 100% of the constant F levels that maximized harvest (Fig. 4). When results for the variable F policies were compared to the constant F frontiers, it was clear that the reduction in variance was much greater than could be accounted for by the lower yield

Table 4

Comparison of average rockfish catches and year-100 variances for constant F, single-species variable F, and multispecies harvesting policies. CVs for biomass estimates were assumed to be 25%.

			Mean yield						Var[100]					
Species	Harvesting policy	Objective function	bocaccio	chili-pepper	widow	split-nose	short-belly	total	bocaccio	chili-pepper	widow	split-nose	short-belly	total
Two	const F	maxh	3.01	2.95	—	—	—	5.97	1.66	2.05	—	—	—	4.10
		logh	3.01	2.95	—	—	—	5.96	1.65	2.01	—	—	—	4.04
		negx	3.01	2.95	—	—	—	5.96	1.64	2.00	—	—	—	4.02
	variable F	maxh	3.04	3.00	—	—	—	6.02	3.33	5.57	—	—	—	9.60
		logh	3.01	2.95	—	—	—	5.93	1.28	1.41	—	—	—	3.00
		negx	3.00	2.93	—	—	—	5.91	1.17	1.26	—	—	—	2.72
	multispp.	maxh	3.01	2.95	—	—	—	5.97	1.65	2.06	—	—	—	4.10
		logh	2.99	2.94	—	—	—	5.92	1.79	1.96	—	—	—	2.44
		negx	2.98	2.93	—	—	—	5.90	1.86	1.95	—	—	—	2.25
Three	const F	maxh	3.03	2.94	7.76	—	—	13.72	1.61	2.05	8.58	—	—	11.58
		logh	3.02	2.94	7.75	—	—	13.72	1.61	2.03	8.51	—	—	11.50
		negx	3.02	2.93	7.73	—	—	13.68	1.60	2.00	8.39	—	—	11.34
	variable F	maxh	3.03	2.99	7.84	—	—	13.80	6.48	4.66	11.25	—	—	22.37
		logh	3.04	2.95	7.74	—	—	13.67	1.58	1.78	6.09	—	—	9.01
		negx	3.01	2.92	7.65	—	—	13.53	1.16	1.48	5.16	—	—	7.47
	multispp.	maxh	3.03	2.94	7.76	—	—	13.72	1.61	2.04	8.56	—	—	12.17
		logh	3.01	2.93	7.73	—	—	13.67	1.83	2.15	8.73	—	—	7.97
		negx	2.93	2.88	7.72	—	—	13.53	2.33	2.36	8.39	—	—	6.01
Five	const F	maxh	3.04	2.86	7.84	1.97	20.00	35.56	1.64	1.26	7.06	0.19	108.60	120.11
		logh	3.04	2.86	7.82	1.97	19.92	35.46	1.63	1.25	7.03	0.19	105.84	117.31
		negx	3.03	2.83	7.80	1.91	19.54	34.96	1.62	1.22	6.95	0.18	96.32	107.63
	variable F	maxh	3.05	2.89	7.90	2.33	20.70	36.74	2.88	3.95	14.34	2.75	958.44	987.02
		logh	3.04	2.87	7.84	2.25	19.55	35.43	1.80	1.54	6.71	0.34	66.07	78.42
		negx	2.99	2.82	7.66	2.22	18.10	33.67	1.04	0.84	4.70	0.34	31.20	40.20
	multispp.	maxh	3.01	2.86	7.84	2.00	20.01	35.59	1.71	1.27	7.07	0.19	107.71	115.41
		logh	2.91	2.56	7.35	1.39	19.60	33.66	1.82	1.51	8.72	1.13	110.50	66.74
		negx	2.22	2.31	7.08	1.14	19.47	32.09	2.79	1.77	9.08	1.48	95.97	40.77

obtained. In some cases, the reduction was comparable to the reduction that would be achieved by lowering the CVs for biomass estimates from 50% to 25% or from 25% to 0%. The percent reduction typically increased as the CVs for biomass estimates increased, although the loss in mean yield also increased somewhat (Hightower 1990).

Single-species vs. multispecies policies

When single-species (5) and multispecies (6) policies were compared, the variance for total catch generally was lower for the multispecies policy, except for some cases for the five- species model or when biomass CVs were 50%. In those cases, the better performance of the single-species policy probably was due to the feedback mechanism it contained. For example, in the five-species models, the single-species policies for shortbelly and splitnose rockfish could adapt to the large changes in the size of those stocks. When the five-species model was rerun using five "stocks" having chilipepper life-history characteristics, the variance for total catch was lower for the multispecies policy.

For the single-species policy, the variance of total catch typically was reduced by stabilizing the catch of each individual species (Tables 3–5). For the multispecies policy, reductions in the variance for total catch were sometimes achieved by increasing the variance for some of the less abundant individual species (Tables 3–5). The reduction in variance obtained using policy (6) is consistent with Clark's (1984) prediction that a multispecies system could be managed to reduce the variance of total yield, relative to the variance of the individual yields.

For the multispecies policies, the optimal parameter estimates were relatively insensitive to the objective function and to the CV for biomass estimates (Hightower 1990). The slope parameter $b_{j,1}$ was less than zero for all cases; consequently, fishing pressure varied inversely with the abundance of the other species.

Table 5

Comparison of average rockfish catches and year-100 variances for constant F, single-species variable F, and multispecies harvesting policies. CVs for biomass estimates were assumed to be 50%.

			Mean yield						Var[100]					
Species	Harvesting policy	Objective function	bocaccio	chili-pepper	widow	split-nose	short-belly	total	bocaccio	chili-pepper	widow	split-nose	short-belly	total
Two	const F	maxh	3.00	2.94	—	—	—	5.93	3.40	3.63	—	—	—	7.39
		logh	3.00	2.93	—	—	—	5.93	3.38	3.59	—	—	—	7.33
		negx	2.99	2.93	—	—	—	5.92	3.38	3.58	—	—	—	7.31
	variable F	maxh	3.02	2.97	—	—	—	5.96	8.49	12.36	—	—	—	21.14
		logh	2.97	2.91	—	—	—	5.85	1.84	1.83	—	—	—	4.06
		negx	2.95	2.90	—	—	—	5.83	1.68	1.69	—	—	—	3.77
	multispp.	maxh	3.00	2.94	—	—	—	5.93	3.40	3.65	—	—	—	7.48
		logh	2.96	2.91	—	—	—	5.87	4.04	3.76	—	—	—	4.24
		negx	2.96	2.90	—	—	—	5.86	4.06	3.91	—	—	—	4.09
Three	const F	maxh	3.01	2.92	7.72	—	—	13.65	3.35	4.42	19.06	—	—	24.74
		logh	3.01	2.92	7.72	—	—	13.64	3.35	4.37	19.03	—	—	24.70
		negx	3.01	2.91	7.69	—	—	13.61	3.34	4.30	18.90	—	—	24.53
	variable F	maxh	3.02	2.94	7.78	—	—	13.70	11.44	6.07	33.98	—	—	48.11
		logh	3.00	2.92	7.66	—	—	13.53	2.17	2.64	10.35	—	--	14.49
		negx	2.97	2.88	7.58	—	—	13.37	1.66	2.02	9.47	—	—	12.76
	multispp.	maxh	3.01	2.92	7.72	—	—	13.65	3.43	4.42	18.91	—	—	24.88
		logh	2.97	2.89	7.69	—	—	13.55	4.58	5.09	20.90	—	—	15.79
		negx	2.91	2.84	7.68	—	—	13.43	6.01	5.34	20.42	—	—	13.29
Five	const F	maxh	3.02	2.84	7.80	1.96	19.84	35.32	3.15	3.87	15.26	0.47	192.76	219.04
		logh	3.02	2.84	7.78	1.96	19.73	35.18	3.14	3.85	15.21	0.47	188.46	214.56
		negx	3.02	2.82	7.72	1.95	19.38	34.75	3.16	3.80	14.96	0.47	177.72	203.35
	variable F	maxh	3.03	2.86	7.81	2.18	20.43	36.18	5.26	10.09	120.32	4.15	1356.71	1540.97
		logh	3.02	2.82	7.78	1.43	18.64	33.56	2.90	1.52	11.61	0.54	64.10	84.87
		negx	2.96	2.78	7.51	1.52	17.32	31.96	1.53	1.26	7.28	0.42	43.02	55.69
	multispp.	maxh	3.00	2.84	7.79	1.97	19.91	35.38	3.34	3.88	15.26	0.47	191.10	209.32
		logh	2.92	2.64	7.44	1.57	19.58	34.01	3.58	3.45	18.95	1.68	208.31	135.32
		negx	2.08	2.28	7.05	1.37	19.20	31.84	7.13	4.10	20.26	2.46	173.92	81.64

Particularly in the three- and five-species cases, it appeared that the optimal multispecies strategy was to maintain stable catches for the species accounting for the majority of total yield, such as shortbelly or widow rockfish. Catches of less-abundant species (e.g., bocaccio or splitnose rockfish) varied depending on the abundance of the dominant species. For example, in the five-species case, the annual catch of splitnose rockfish was 0 in 24–30 of 100 years for the logh policies.

Errors in biomass estimates

Constant F policies were essentially identical when different CVs for biomass estimates were used. This indicates that the current management approach for Pacific Coast groundfish is robust to random, non-autocorrelated errors in estimating biomass. One obvious impact in the simulated fishery of introducing errors in estimating biomass was that the variance for total catch increased substantially (Tables 3–5, Fig. 4). This increased variability was due to differences between the intended (F) and actual (F′) fishing mortality rate. Such errors are nonlinearly related to estimated stock size and can be substantial (Rivard 1981). Rivard (1981) argued for higher precision in estimates of stock size in order to reduce the biological risk of applying $F' \gg F$ or the economic loss if $F' \ll F$. In this study, the variation in F due to errors in estimating biomass was much greater than that caused by using the variable F policies. For example, when CV = 0%, Fs for chilipepper in the five-species case ranged from 0.00 to 0.24 when using the multispecies logh model. When CV = 25%, the actual Fs ranged from 0.06 to 0.61 when the intended policy was a constant F of 0.22. Actual Fs ranged from 0.00 to 0.63 when CV = 25% and a multispecies logh policy was used, which suggests that multispecies policies do not introduce substantial additional risk, relative to the risk introduced by estimating biomass with error.

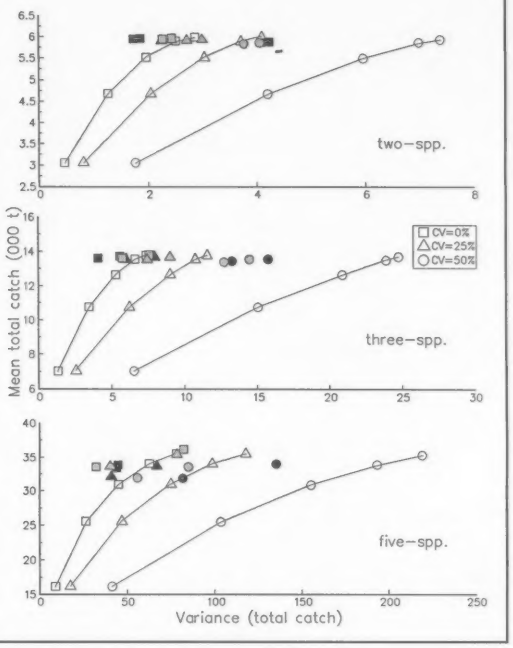

Figure 4

Relationship between mean total rockfish catch and the variance of total catch for the two- (bocaccio, chilipepper), three- (bocaccio, chilipepper, widow rockfish), and five-species (bocaccio, chilipepper, widow, splitnose, and shortbelly rockfish) models. Open symbols represent Pareto Frontiers derived by simulating the fishery at 20, 40, 60, 80, and 100% of the constant fishing mortality rate (F) that maximized harvest. Shaded and closed symbols represent the catch:variance relationship for the variable F and multispecies policies, respectively (equations 5–6). Simulation runs were made assuming a 0, 25, or 50% coefficient of variation for annual estimates of stock size.

Table 6

Average total rockfish catches and year-100 variances for constant F, variable F, multispecies, and three-parameter harvesting policies for the three-species model.

Biomass CVs	Policy	Objective function	Yield	Var[100]
0	(4)	maxh	13.75	7.40
	(5)	logh	13.78	7.59
	(6)	logh	13.70	5.60
	(7)	logh	13.77	6.39
	(5)	negx	13.61	5.75
	(6)	negx	13.60	4.08
	(7)	negx	13.60	4.09
25	(4)	maxh	13.72	11.58
	(5)	logh	13.67	9.01
	(6)	logh	13.67	7.97
	(7)	logh	13.63	6.99
	(5)	negx	13.53	7.47
	(6)	negx	13.53	6.01
	(7)	negx	13.51	5.40
50	(4)	maxh	13.70	24.74
	(5)	logh	13.53	14.49
	(6)	logh	13.55	15.79
	(7)	logh	13.50	11.39
	(5)	negx	13.37	12.76
	(6)	negx	13.43	13.29
	(7)	negx	13.33	8.21

Mean yield was only slightly lower at higher biomass CVs; the decrease was similar for constant F and variable F policies (Tables 3–5). Thus, in this model at least, there was no apparent disadvantage in using the more complex policies, even when biomass was estimated imprecisely. This was an interesting result because, although all policies used biomass estimates to calculate catch, the variable F policies also use the estimates to calculate Fs.

When biomass CVs were 50%, the variance for total catch was in all cases lower for the single-species (5) than for the multispecies policy (6). Apparently it was important to readjust continuously for the changes in stock size due to previous errors in estimating biomass. Based on limited additional runs using the three-species model, it appears that further gains in stability of total catch could be achieved by using a three-parameter harvesting policy (Table 6):

$$F_j[t] = b_{j,0} + b_{j,1} B_j[t] / B_{\infty,j} + b_{j,2} \sum_{i \neq j} B_i[t] / \sum_{i \neq j} B_{\infty,i}. \quad (7)$$

The primary disadvantage of this policy is the computational expense required to obtain the policy parameter estimates.

Model limitations

One of the primary assumptions underlying this model is that trawlers can, on an annual basis, control the relative proportions of the individual rockfish species in the catch. That appears to be a reasonable assumption for widow rockfish, which are caught primarily in a directed midwater trawl fishery. Catches of other rockfish species should be low in a midwater trawl fishery for shortbelly rockfish (Lenarz 1980), and the Pacific Fishery Management Council is unlikely to permit a bottomtrawl fishery for that species. Peak abundance of splitnose rockfish is in deeper water than for the other species used in this model; however, some

catches (particularly in the 100–149 fm depth interval) would likely contain bocaccio and chilipepper as well (Gunderson and Sample 1980). The greatest degree of overlap would be for bocaccio and chilipepper. Bocaccio occur over a greater latitudinal range than chilipepper, but in the area off California where both species are abundant, it could be difficult to maintain markedly different catch levels for the two species. An improved version of this model would incorporate probabilities for different levels of bycatch, so that the optimal policies would be constrained by the degree of targeting that was feasible (Pope 1979).

Another important assumption is that the species included in the objective function are interchangeable in the marketplace. That is a valid assumption for the commerically important *Sebastes* species, including widow rockfish, bocaccio, and chilipepper. However, demand for splitnose rockfish has been low because of its small size and low fillet yield (Lenarz 1986). A low price would be expected for shortbelly rockfish because they are small in size and must be processed rapidly (Lenarz 1986). Lenarz (1986) suggested that better marketing approaches will be needed before significant quantities of either splitnose or shortbelly rockfish can be harvested. For the model used in this study, differences in price among species could be accommodated easily and the objective function could be modified to maximize some function of income. It would also be of practical importance to determine whether all vessels participating in these fisheries caught all the species used in the objective function. Policies that result in variable catches of the species used in the model would be less appropriate if some fishermen did not catch or were unable to market some of the species.

The objective function could also be modified to include costs of fishing (see, for example, Pikitch 1987). However, the current practice of the Pacific Fishery Management Council is to manage for maximum sustainable yield; costs of fishing are not considered. Stock assessments are restricted to estimation of Acceptable Biological Catch (ABC), and the Council considers some socioeconomic factors when determining "Optimum Yield" from the ABC.

A limitation of this study was the assumption that model parameters M, B_∞, and A were known. Those parameters strongly affect equilibrium yields; consequently, when they are not well estimated, the passive policies used in this study might be outperformed by an adaptive probing strategy (Walters 1986). Under such a strategy, short-term fluctuations in fishing mortality and yield would be accepted in order to better estimate the productivity of the stock and improve long-term management.

Another potential limitation of the model used in this study was the assumption that errors in estimating biomass were not autocorrelated. That assumption may be valid when estimates are based on methods such as a swept-area trawl survey, although the fishery manager would be expected to balance any single estimate of stock size against observations from prior years. Autocorrelated errors would be likely in cases where estimates were based on a time-series of catch data. Such errors would be expected to have more serious consequences than the independent errors assumed here. An approach for introducing autocorrelated errors might be to use CVs of the same magnitude as assumed here but to use a 2- or 3-year moving-average estimate of biomass to set quotas. Errors in estimating biomass might also be correlated among species; for example, swept-area trawl surveys may underestimate the biomass of several species.

A possible limitation of this model was the assumption that the reliability of assessment data was equivalant for all species. If differences in the reliability of estimates were substantial, it might be found that a reliable single-species policy would be preferable to a multispecies policy that incorporated unreliable information on additional species.

Summary

1 When constant F policies for different objective functions were compared, the optimal F, total yield, and variance for total yield decreased as the level of risk aversion increased.

2 Single-species and multispecies variable F policies for maximizing harvest did not increase total yield significantly compared with constant F policies.

3 Single-species and multispecies variable F policies for the logh and negx objective functions provided a substantial reduction in the variance of total yield, compared with a constant F policy for maximizing harvest.

4 For the logh and negx objective functions, the variance for total catch was lower for the multispecies than for the single-species variable F policies, except for some cases for a five-species model or when biomass CVs were 50%.

5 Constant F policies for maximizing harvest (the current management approach) were essentially identical for different levels of random, non-autocorrelated errors in estimating biomass. Mean yield was slightly lower at higher biomass CVs for both constant F and variable F policies.

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Use of Otolith Microchemistry to Distinguish the Progeny of Sympatric Anadromous and Non-anadromous Salmonids

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Abstract.—Otolith microchemistry of anadromous and non-anadromous salmonids was investigated to determine if there were differences among migratory and nonmigratory individuals and if the habitat where vitellogenesis took place would affect the composition of the otolith primordia of the progeny. Electron microprobe transects across salmonid otoliths showed that there were large differences in otolith Sr/Ca ratios among adult anadromous and non-anadromous individuals, but there were no detectable differences in Na/Ca, K/Ca, and S/Ca ratios. The hypothesis that Sr/Ca ratios in the primordia of the progeny of anadromous salmonids would be greater than those in the primordia of the progeny of non-anadromous individuals because of differences in the composition of ova was tested and confirmed by the results of a controlled experiment. Also, the ova of anadromous *Oncorhynchus mykiss* were found to contain 5 times more Sr than their non-anadromous conspecifics. On the basis of these data, it was concluded that otolith nucleus Sr/Ca ratios can be used to distinguish the progeny of sympatric anadromous and non-anadromous salmonids.

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The ability to differentiate between juvenile anadromous salmonids and their sympatric non-anadromous conspecifics is essential for management of these species. However, stock discrimination between sea-run and resident freshwater salmonids has been limited to the adults upon their return from the sea to spawn. Furthermore, for those species where anadromy is a facultative, and not an obligate behavior, such as brown trout *Salmo trutta*, rainbow trout *Oncorhynchus mykiss*, Atlantic salmon *Salmo salar*, cutthroat trout *Salmo clarkii*, and Arctic char *Salvelinus alpinus*, it has been impossible to distinguish between the co-occurring forms on the basis of meristic or morphometric characters (Nordeng 1983, Jonsson 1985, Neilson et al. 1985). McKern et al. (1974) were able to distinguish between winter and summer races of steelhead trout (anadromous rainbow trout) from rivers in British Columbia, Washington, and Oregon on the basis of sagittal otolith nuclear dimensions that they believed to be affected by both qualitative and quantative differences in yolk. Rybock et al. (1975) concluded that differences in the size of female resident non-anadromous rainbow trout and steelhead trout resulted in differences in egg size and, subsequently, the size of the otolith nucleus in the progeny. However, both Neilson et al. (1985) and Currens et al. (1988) found that measurements of otolith nuclear dimensions were of questionable value in distinguishing juvenile non-anadromous and anadromous rainbow trout.

Development of ova in anadromous salmonids is virtually complete through vitellogenesis or yolk formation before the fish enter freshwater. On the basis of this information, I hypothesized that egg composition would, in some way, reflect the chemical composition of the seawater environment and that this would ultimately affect the composition of the otoliths of the progeny, particularly the otolith nuclei that are formed in the early stages of development and well before yolk utilization is complete. Yolk is formed through the deposition of a phospholipoprotein-calcium complex yolk precursor, vitellogenin, in the developing oocyte (Mommsen and Walsh 1988). Solubility and transport of vitellogenin through the circulatory system of the female and to the developing ovaries may be dependent on the presence of calcium which has been shown to increase markedly in female salmonids (Bailey 1957, Booke 1964, Elliot et al. 1979) and other fishes (Oguri and Takada 1967, Woodhead 1968) during gonad development. Vitellogenin has a high affinity for calcium due to the significant negatively-charged phosphate component of the molecule (Hara and Hirai 1978, Hara et al. 1980). The calcium binds to the vitellogenin molecule and, in this complexed form, the vitellogenin and calcium are deposited in

the oocyte. Clearly, yolk deposition is a conservative process in that the overall composition of the yolk is more dependent on the genetic programming of the female parent than the environment. However, in many calcium-binding proteins, such as vitellogenin, the calcium moiety of the complexed molecule can be substituted by strontium due to the similar structural features of Ca^{++} and Sr^{++} (Skoryna 1981). The relative degree of this substitution would be largely dependent on the relative concentrations of calcium and strontium in the ambient environment. Typical Sr/Ca ratios in marine waters (salinity 35‰) are 0.0087 (0.09 mM/kg Sr:10.3 mM/kg Ca) (Bruland 1983) and average 0.0019 (0.00068 mM/kg Sr:0.35 mM/kg Ca) in freshwater (Rosenthal et al. 1970). These differences would be expected to affect the Sr/Ca ratio of the yolk and, ultimately, the composition of the developing embryo and its otoliths.

In a study of otolith and endolymph composition, Kalish (1989) showed that the quantity of strontium incorporated into the otolith was directly related to the quantity of strontium present in the endolymph, and that anadromous brown trout collected in an estuary had higher levels of strontium in both the endolymph and otolith than non-anadromous brown trout. Therefore, it seems likely that differences in the elemental constituents of the yolk and embryos of anadromous and non-anadromous salmonids would result in differences in otolith composition. This hypothesis is supported by research that shows little or no exchange of calcium between prehatch salmonid embryos and the environment (Hayes et al. 1946, Zeitoun et al. 1976). This would be expected since calcium present in the yolk of the developing embryo is probably present in a protein-bound form and is destined for the tissues of the fry. Craik and Harvey (1984) found that the calcium composition measured in whole rainbow trout eggs was indistinguishable from the calcium measured in protein precipitate obtained from the egg. This, of course, excludes calcium that would be present in the fluid of the perivitelline space following fertilization (Laale 1980, Alderdice 1988). Strontium would probably behave similarly and there would be minimal loss of any seawater-derived protein-bound ions in the yolk to the freshwater environment where the development of salmonid embryos takes place.

In this paper, I discuss variations in the elemental composition of the otoliths of non-anadromous and anadromous salmonids with emphasis on the composition of the sagittal otolith nucleus. Several "life history" transects (scans of elemental composition across an axis of an otolith made with a wavelength-dispersive electron microprobe) are presented to indicate the variety of forms that these data may take in salmonids with differing life histories. I also present the results of an experiment designed to test the hypothesis that otolith primordia of the progeny of anadromous rainbow trout contain higher levels of strontium than the otolith primordia of non-anadromous rainbow trout. These data are examined in view of their usefulness in distinguishing the progeny of sympatric non-anadromous and anadromous salmonids and in investigations of diadromous behavior.

Methods

Brown trout (non-anadromous *Salmo trutta*) and sea trout (anadromous *Salmo trutta*) were collected by gillnet from the Derwent River and estuary, southeast Tasmania, Australia. Juvenile and adult rainbow trout were obtained from both wild and hatchery stock. Atlantic salmon were obtained from hatcheries. Otoliths were removed from fresh fish, cleaned, and stored in glass vials. Details of otolith preparation and microprobe analyses are described below.

Ripe ova were obtained from ovulating freshwater rainbow trout and sea-farmed rainbow trout and frozen in plastic bags for later analyses of calcium and strontium. Whole rainbow trout eggs were used for the determinations. Groups of 10 eggs from 4 freshwater and 4 sea-farmed trout were used. Preparation of eggs was modified from the methods employed by Craik and Harvey (1984). All solutions were made up with Milli-Q water (Millipore Corp.). Groups of eggs were weighed wet and then oven-dried at 50°C for 24 hours to estimate dry weight. The dried whole eggs were ashed at 500°C for 24 hours and then digested in 2.0 mL Aristar ultrapure hydrochloric acid at 100°C for 2 hours. Samples were separated into two equal aliquots for separate calcium and strontium determinations. Sample digests for estimation of calcium were diluted in 10 mM lanthanum chloride to suppress interference due to phosphate binding. Calcium concentrations were determined by flame atomic absorption spectrophotometry using an air-acetylene flame.

Strontium concentrations in eggs were determined by the method of standard additions using graphite furnace atomic absorption spectrophotometry on a Varian AA-1475 spectrophotometer equipped with a GTA-95 graphite furnace and an autosampler. Argon was used as the purging gas in the graphite furnace. Samples were diluted with a 0.25% solution of an ionic detergent, Triton X-100, and 20 μL of diluted sample were injected by autosampler into a walled, pyrolytically coated graphite tube. Furnace conditions were: drying

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Electron microprobe analytical data for salmonid otolith analyses. Details of counting times, counting precision, and materials used as standards. Calculation of the counting precision is discussed in Goldstein et al. (1981). Precision values are for the 95% confidence level.

Spectrometer/ crystal	Element	Peak counting time (sec)	Counting precision	Standard material	Source
1/PET	Ca-K_α	10	~28,000 counts collected 1.0%	Calcite	USNM* 136321 Jarosewich and MacIntyre (1983)
1/PET	K-K_α	30	15% when $K/Ca = 2 \times 10^{-3}$	Anorthite	USNM 137041 Jarosewich et al. (1980)
2/PET	S-K_α	40	36% when $S/Ca = 1 \times 10^{-3}$	Troilite	BMR** Museum Ramdohr and Goresy (1971)
3/TAP	Na-K_α	20	8.1% when $Na/Ca = 2 \times 10^{-2}$	Anorthite	Same as for K above
3/TAP	Sr-L_α	20	9.9% when $Sr/Ca = 3 \times 10^{-3}$	Strontianite	USNM 10065 Jarosewich and White (1987)

*Natl. Mus. Nat. Hist., Smithsonian Inst., Wash., DC
**Bur. Miner. Resour., Canberra, Australia

at 90°C for 60 seconds; ramp ashing from 90 to 700°C for 20 seconds; ashing at 2600°C for 1 second; and atomization, with no gas flow, at 2600°C for 3 seconds.

To confirm the hypothesis regarding otolith nucleus composition, eggs were obtained from sea-farmed and freshwater broodstock rainbow trout which originated from a similar hatchery stock (Cressy, Tasmania). These two groups of hatchery fish derive from similar stocks of rainbow trout imported into Tasmania; because of minimal gene flow, inbreeding is relatively great and the diversity of the gene pool is low. Both freshwater and sea-farmed adults had been maintained on jack mackerel *Trachurus declivis* based pellets throughout the period of egg development. Sea-farmed broodstock were kept at the same hatchery as freshwater broodstock for 3 weeks before stripping, and all eggs were fertilized with sperm from a male of freshwater stock. The developing embryos from sea-farmed and freshwater broodstock were maintained in separate baskets in the same channel of a recirculating water system where temperature was maintained at 10°C. A natural photoperiod was maintained throughout the experiment. A random sample of 20 freshwater progeny and 20 sea-farmed progeny was taken 20 days after hatching, and these fish were frozen for later removal of otoliths. Sagittae and lapilli were removed from fry, the adhering otolith capsule was removed, and otoliths were rinsed in deionized water. Otoliths were oven-dried at 40°C. The length of sagittae and lapilli was measured with an ocular micrometer.

Otoliths from adults were embedded in Araldite D epoxy resin (Ciba-Geigy) and polymerized in an oven at 40°C for 48 hours. Several transverse sections of approximately 200 μm thickness were obtained from otoliths, including one section containing the primordium, with a low-speed saw (Struers Accutom) equipped with a diamond cut-off wheel. Sections were affixed to glass slides with epoxy. After drying, sections were ground with a graded series of carborundum paper (wet/dry paper 600–1200 grade) until the primordia were reached. The much smaller otoliths from fry were mounted, sulcus-side-up, in Crystalbond 509 (Aremco Products, Inc.), a heat-labile thermoplastic polymer (Neilson and Geen 1981), and ground in the sagittal plane to the level of the primordia with 1200-grade wet-dry paper. All otoliths were then ground to the precise level of the primordia on a lapping wheel with 0.25 μm aluminium paste (Linde A) and then finished with 0.25 μm diamond paste. Polished specimens were ultrasonically cleaned in reagent-grade mineral spirits followed by ultrasonic cleaning in deionized water and oven drying at 60°C. Samples were then coated in a high-vacuum evaporator with a 25-nm carbon layer and stored in a dessicator.

Otolith elemental analyses were carried out with a Cameca SX-50 wavelength-dispersive electron microprobe. Analyses were made with a square raster of 10×10 μm. Probe current and accelerating voltage were 10 nA (measured on Cu) and 15 kV, respectively. Elements analyzed included Ca, Sr, Na, K, and S. Salmonid otoliths are very susceptible to damage from the electron beam, and it was necessary to utilize a low-beam current and reduced counting times for all analyses. In conjunction with these conditions that reduce the total number of X-ray counts from a specimen, it is important to be aware of detection limits and counting statistics. A treatment of these subjects can be found in Goldstein et al. (1981) and references therein.

Details of the microprobe counting procedures, precision, and standards employed in this study are outlined in Table 1. Background was measured at offsets both above and below peak position for 50% of the peak counting time. The average counts from these two background measurements were subtracted from the peak. Background measurements were made with each analysis. Corrected X-ray intensity ratios were calculated using the ZAF method (Reed 1975), and the final elemental ratios are normalized atom ratios based on concentrations derived from the standards.

Elemental data for otolith life-history transects from adult salmonids were collected with approximately 40 μm separating each 10×10 μm sample region (50 μm separating the center point of each sample). This sampling spatial frequency was judged to be adequate because it was desired to collect data relating to major life-history changes only, and not recurring or seasonal events.

For a comparison of otolith composition among the progeny of sea-farmed fish and freshwater fish, microprobe data were collected from five individual primordia within each sagitta or lapillus. In some lapilli it was necessary to make multiple measurements on individual primordia because five primordia were not always exposed or visible. In addition, five microprobe measurements were made on each otolith at points near the otolith edge that were indicative of the otolith composition at a time after the completion of yolk absorption.

Results

Otolith life-history transects representative of several types of adult salmonids are presented in Figure 1. Differences in otolith transects among anadromous or sea-farmed fish and non-anadromous individuals are only evident in the Sr/Ca data and, therefore, only Sr/Ca life-history transects are presented. Sea trout, sea-farmed Atlantic salmon, and sea-farmed rainbow trout exposed to the marine environment display a clear increase in otolith Sr/Ca that is coincident with entry into seawater.

There is an initial peak, associated with the otolith nucleus, in the Sr/Ca ratio of the sea trout and Atlantic salmon, but this peak does not appear in the sea-farmed or freshwater rainbow trout. In Tasmania, freshwater broodstock are used for the production of sea-farmed rainbow trout. The peak in otolith Sr/Ca in the otolith nucleus of some individuals is presumably due to the presence of strontium sequestered in the egg yolk proteins during the seawater phase of ovarian development of the fishes' female parent.

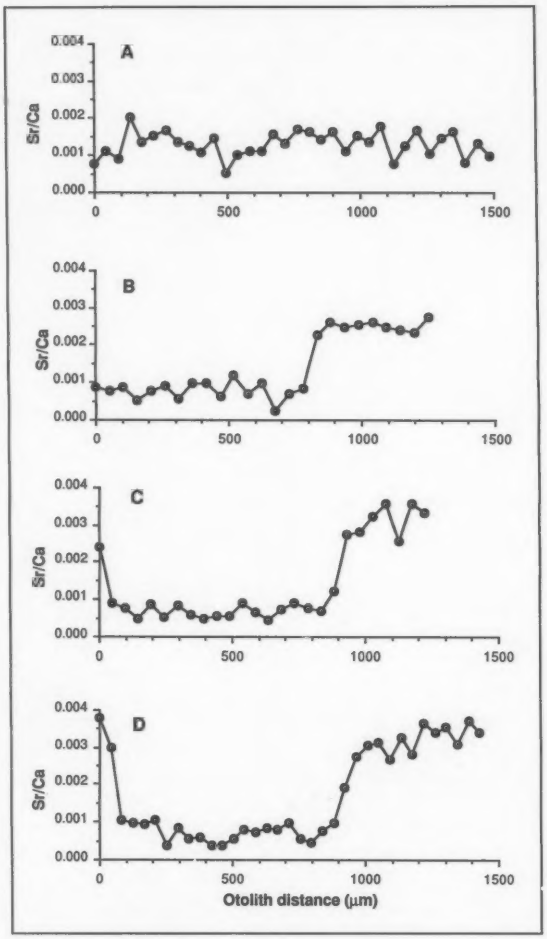

Figure 1

Transects of otolith Sr/Ca ratios measured with a wavelength-dispersive electron microprobe from the primordium (0 μm) to the otolith edge along transverse sections of sagittae from 4 female adult salmonids with differing life histories. Each point represents a single measurement made over an area of 100 μm^2. (A) Wild non-anadromous *Oncorhynchus mykiss* from Great Lake, Tasmania; (B) sea-farmed *Oncorhynchus mykiss*; (C) sea-farmed *Salmo salar*; and (D) wild anadromous *Salmo trutta* from the Derwent River estuary.

The hypothesis that the seawater strontium contribution to the egg would result in increased otolith strontium was confirmed by the results of the rearing experiment. Results of this experiment are presented in Table 2. Mean Sr/Ca ratios based on measurements in five primordia from each of the 20 sea-farmed broodstock progeny was 0.00313 ± 0.00068, significantly greater than the mean value of 0.00114 ± 0.00014 measured in the primordia of the freshwater brood-

Table 2

Mean elemental ratios measured in primordia and post-yolk absorption regions in the sagittae and lapilli of progeny of sea-farmed and freshwater rainbow trout *Oncorhynchus mykiss*. Values are means ±1 standard deviation based on 5 microprobe measurements in the nucleus and post-yolk absorption regions of each otolith. $N = 20$ for sagittae, and $N = 5$ for lapilli. Significance tests alongside sagittae and lapilli primordia data are the results of paired two-tailed t-tests between those otolith primordia and the post-yolk absorption regions of the same otoliths.

	Sr/Ca ($\times 10^2$)	Na/Ca ($\times 10^2$)	K/Ca ($\times 10^3$)	S/Ca ($\times 10^3$)
Sea-farmed progeny				
Sagittae ($N = 20$)				
Primordia	3.13 ± 0.68***	2.03 ± 0.16***	2.07 ± 0.47***	1.65 ± 0.63**
Post-yolk absorption	1.07 ± 0.31	1.86 ± 0.16	2.62 ± 0.52	1.08 ± 0.21
Lapilli ($N = 5$)				
Primordia	4.34 ± 0.80**	1.98 ± 0.09*	1.84 ± 0.30*	1.30 ± 0.35 ns
Post-yolk absorption	0.83 ± 0.24	1.74 ± 0.06	2.30 ± 0.07	1.00 ± 0.14
Freshwater progeny				
Sagittae ($N = 20$)				
Primordia	1.14 ± 0.14 ns	2.10 ± 0.08***	2.61 ± 0.41 ns	1.75 ± 0.38***
Post-yolk absorption	0.96 ± 0.19	1.73 ± 0.15	2.46 ± 0.37	1.21 ± 0.21
Lapilli ($N = 5$)				
Primordia	1.20 ± 0.18 ns	1.95 ± 0.04*	2.43 ± 0.25 ns	1.32 ± 0.14 ns
Post-yolk absorption	1.06 ± 0.13	1.72 ± 0.06	2.68 ± 0.26	1.27 ± 0.27

*$P \leq 0.01$; **$P \leq 0.001$; ***$P \leq 0.0001$; ns = not significant ($P > 0.05$).

stock progeny (unpaired one-tailed t-test, $t = 12.69$, $P < 0.0001$). One-way analysis of variance showed that there were no significant differences in mean otolith primordia Sr/Ca ratios among individuals from either seawater ($F = 0.88$, $P = 0.476$) or freshwater broodstock ($F = 1.29$, $P = 0.279$). Differences in otolith primordia composition between sea-farmed progeny and freshwater progeny were not significant for Na/Ca (unpaired two-tailed t-tests, $t = 1.82$, $P = 0.076$) and S/Ca ($t = 0.58$, $P = 0.568$), but were significant for K/Ca ratios ($t = 3.88$, $P = 0.0004$). Similar results were obtained for measurements made in lapilli primordia from five freshwater and five marine progeny. Table 2 also presents the results of comparisons between the composition of the nucleus and post-yolk absorption regions of the otoliths.

A histogram of the frequency distribution of Sr/Ca ratios determined for five primordia in the sagittae of 20 progeny of sea-farmed rainbow trout and 20 progeny of freshwater rainbow trout shows that there is little overlap between individual measurements from the two groups (Fig. 2). Only 5% of the measurements from the sea-farmed progeny overlap with 13% of the freshwater progeny measurements. A frequency histogram of the mean Sr/Ca ratios obtained from each sagitta nucleus shows that the sea-farmed and freshwater progeny are clearly separated on the basis of otolith primordia Sr/Ca ratios (Fig. 2).

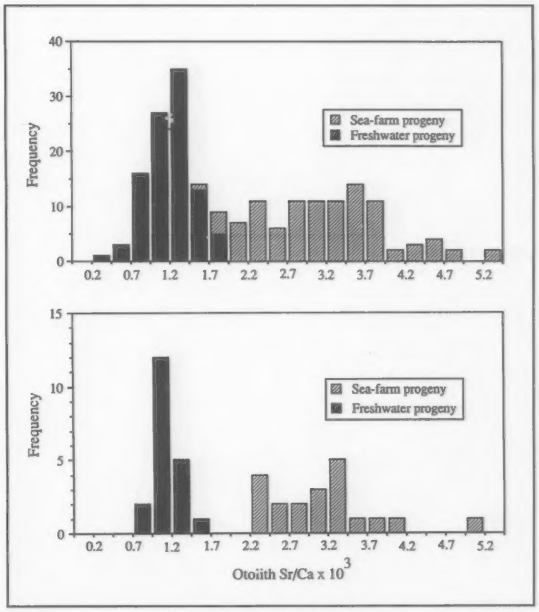

Figure 2

(Above) Frequency distribution of individual otolith Sr/Ca measurements made in the primordia of 20 sagittae from *Oncorhynchus mykiss* fry of sea-farmed broodstock and 20 sagittae from fry of freshwater broodstock ($N = 200$), and (below) frequency distribution of mean otolith Sr/Ca ratios from the same 40 sagittae.

Measurements of otolith composition made in regions of the sagittae formed after the completion of yolksac absorption and corresponding with a period soon after first feeding corroborated data that showed the influence of yolk on otolith composition. There were no significant differences in Sr/Ca (unpaired two-tailed t-tests, $t = 1.30$, $P = 0.201$), S/Ca ($t = 2.02$, $P = 0.051$), or K/Ca ($t = 1.09$, $P = 0.282$) ratios measured in the later-formed regions of the otoliths from the two groups of fry and only slightly significant differences for Na/Ca ratios ($t = 2.70$, $P = 0.010$). Differences between the Sr/Ca ratio of the sagitta edge and primordium were highly significant in the sea-farmed broodstock progeny (paired two-tailed t-tests, $t = 10.38$, $P<0.0001$), and only slightly significant in the progeny of the freshwater broodstock ($t = 3.13$, $P = 0.003$).

Six electron microprobe transects over a sagitta from a single *Oncorhynchus mykiss* fry of sea-farmed broodstock origin were made to show Sr/Ca ratios over the entire otolith including the nucleus and pre- and post-yolk absorption regions (Fig. 3). The outermost points towards the otolith rostrum and posterior show the sagitta Sr/Ca ratios after the completion of yolksac absorption and provide evidence for much reduced otolith Sr/Ca ratios when compared with the otolith material produced during the period of yolksac utilization. The data also indicate that, in general, high Sr/Ca ratios prevail throughout the region of the nucleus and are not confined to the primordia alone.

Measurements of egg calcium and strontium composition show that ova of the sea-farmed rainbow trout contain higher levels of strontium than their freshwater conspecifics. The mean strontium content was 0.054 ± 0.013 μM/g of ova (dry weight) for ova that had developed in seawater and 0.010 ± 0.002 μM/g for ova from freshwater fish, and the difference between these values was significant (unpaired two-tailed t-test, $t = 6.60$, $P = 0.0006$). Mean calcium content of yolk was 0.035 ± 0.005 mM/g from sea-farmed broodstock and 0.026 ± 0.004 mM/g from freshwater fish and these values were also significantly different ($t = 3.06$, $P = 0.022$).

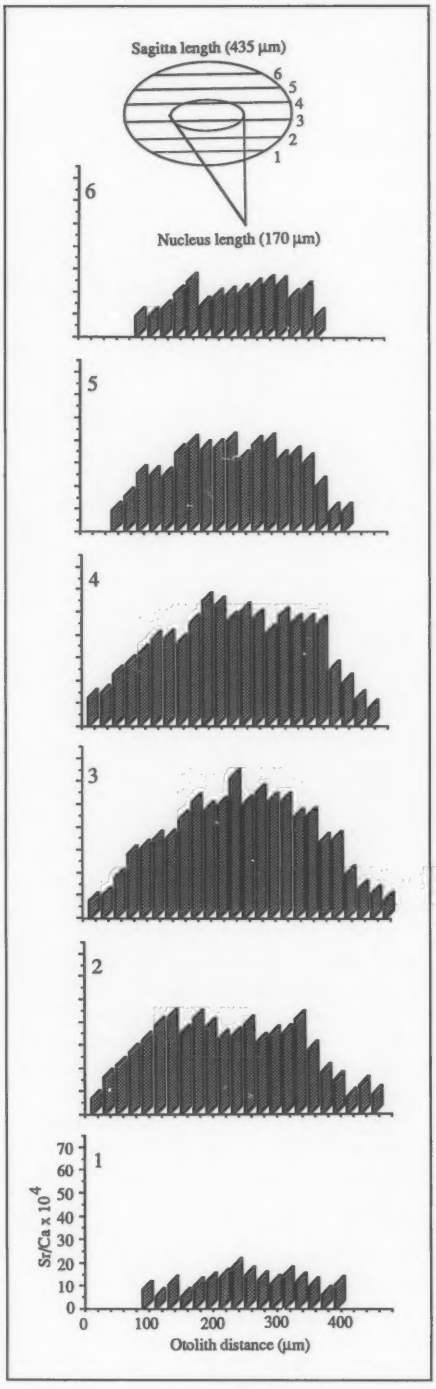

Figure 3

Six transects of otolith Sr/Ca ratios made with a wavelength-dispersive electron microprobe on a single sagitta from an *Oncorhynchus mykiss* fry of sea-farmed broodstock origin. The otolith was ground to the level of the primordia in the sagittal plane. Each column in the histograms represents an individual microprobe measurement ($N = 120$). Outermost points show the sagitta Sr/Ca ratios after the completion of yolksac absorption.

Discussion

The results present evidence that the Sr/Ca ratios of otolith primordia formed during embryonic development are directly influenced by the strontium content of the individual's yolk and that yolk composition is also influenced by the composition of the waters where vitellogenesis took place. These findings are important to the study and management of salmonid species where anadromy is a faculative behavior. They may also be important to studies of other diadromous species, but it remains to be seen whether the relatively small nutritive contribution of the yolk in these fishes is adequate to influence otolith composition. However, since otolith primordia develop very early in the ontogeny of fishes (Brothers 1984), there may be detectable differences in otolith strontium content within other species that display facultative diadromy. In many cases, the analysis of otolith primordium composition should make it possible to investigate the relative importance of parentage and environment in determining diadromous behavior.

The basis for the differences in otolith primordium composition among anadromous and non-anadromous fishes is such that there is probably little, if any, effect of race or population. Both wild and hatchery salmonids involved in this study displayed similar ranges of elemental ratios, depending on habitat (freshwater or marine) indicating that different salmonid species may incorporate into their otoliths a similar proportion of the ions present in the endolymph. Furthermore, this indicates that the relationship between endolymph and blood plasma composition is regulated in a similar manner in each of these species. Kalish (1989) showed that there was a tendency for both endolymph and otolith Sr/Ca ratios to be similar among individuals of a species, whereas differences were greatest among species. On the basis of the data presented here and in Kalish (1989), it seems likely that freshwater and marine salmonid otolith Sr content could be predicted on the basis of endolymph composition.

The results of this study confirm that differences in the composition of freshwater and seawater can be reflected in the composition of fish otoliths. These findings are similar to those obtained by Casselman (1982), Radtke et al. (1988), and Kalish (1989). Wavelength-dispersive electron microprobe analyses of strontium content in diadromous fish otoliths can provide information on the rates of migration to and from the sea, residence times at sea and in freshwater, the age at which migrations take place, and confirmation of data obtained from scales.

Confirmation of data obtained from scale reading is important because of the possibility of scale resorption (Bilton 1974) and the equivocal nature of data obtained from scales in the discrimination of adult anadromous and non-anadromous salmonids. Bagenal et al. (1973) used the strontium content of whole scales to distinguish between brown trout and sea trout, and Moreau and Barbeau (1979) used a similar rationale to discriminate anadromous from non-anadromous whitefish *Coregonus clupeaformis*. However, Castonguay and FitzGerald (1982) found that this method was unreliable for distinguishing between anadromous and non-anadromous brook char *Salvelinus fontinalis*, and Gausen and Berg (1988) had similar results when investigating migratory and non-migratory Atlantic salmon. Measurements of otolith Sr may provide a more reliable means of determining migratory behavior in these species because otoliths are not resorbed during periods of stress (Simkiss 1974, Campana 1983), although Mugiya and Uchimura (1989) present evidence for otolith resorption in goldfish *Carassius auratus* during extreme anaerobic stress. Also, otolith Ca and, most likely, Sr are derived from ions taken up by the gills (Simkiss 1974), and any variations in the Sr content of the diet would not be reflected in the composition of the otoliths. This is not the case for scales, and differences in the Sr content of the diet as well as the effect of different levels of discrimination against Sr would be manifested in scale composition.

It is important to point out the inadequacy of energy-dispersive (ED) electron microprobe analysis for the determination of Sr at the levels typically found in marine fish otoliths and particularly in the otoliths of freshwater species. Under optimal operating conditions, the minimum detectability limit for a wavelength-dispersive (WD) electron microprobe is approximately 10 times lower than that of an ED microprobe for all elements (Geller 1977, Goldstein et al. 1981). Generally, the minimum detection limits attainable with an ED spectrometer are on the order of 0.10% wt (1000 ppm), and these conditions are frequently not realized due to various factors. The range of Sr concentrations measured in this study was approximately 300–5000 ppm, and all marine fish otoliths investigated to date appear to contain Sr in excess of 1000 ppm (Radtke 1987, Edmonds et al. 1989, Kalish 1989). Theoretically the ED spectrometer should be capable of making all otolith Sr measurements in marine fish and some of those from freshwater fish. However, the detection and accurate quantitative estimation of Sr creates special problems for the ED microprobe.

The X-ray line that is used to detect Sr at 1.806 keV (L_α) is affected by the silicon escape peak associated with the large Ca K_α peak produced when measuring specimens that are largely calcium (aragonite fish otoliths are approximately 38% wt Ca). The silicon escape peak results from the production of Si K_α photons following absorption of relatively high energy (>1.841

keV) photons by the silicon detector of an ED spectrometer (Reed and Ware 1972). The energy of the photon producing the escape peak is $E_x - E_{Si}$, where E_x is the incident photon energy and E_{Si} is the energy of a Si K_α photon (1.739 keV). The silicon escape peak due to Ca K_α would have an energy of 1.951 keV (3.690 keV – 1.739 keV) and an intensity 0.78% that of the Ca K_α peak (Reed 1975). Such a peak, within less than 150 eV of the Sr peak, would create significant errors in the estimation of low levels of Sr. Measurements of trace levels of phosphorus with the K_α line (2.013 keV) would be even more vulnerable to errors because of the closer proximity to the Ca K_α derived silicon escape peak. Other errors can result from a silicon internal fluorescence peak (Reed and Ware 1972) and the silicon absorption edge (Goldstein et al. 1981, Statham 1981), both artifacts of the ED spectrometer and associated silicon detector, and of particular interest to the determination of trace levels of Sr. These sources of error are not present when using a WD electron microprobe.

There are numerous other potential sources of error in otolith trace-element studies carried out with ED electron microprobes. These errors can occur due to the relatively poor energy resolution of the ED spectrometer and the resultant inability to discriminate between X-ray lines separated by less than approximately 150 ev (Statham 1981). Furthermore, the presence of a greater proportion of continuum background radiation or "bremsstrahlung" in the ED spectrometer, due to decreased energy resolution, results in a fivefold increase in the peak to background ratio in a WD spectrometer over an ED spectrometer (Reed 1975). These factors, and others, make it necessary to view with caution studies with ED microprobes that investigate the distribution of large numbers of trace (<0.5% wt) elements, particularly without reference to criteria for determining detection levels or precision. In an investigation of otolith composition using X-ray fluorescence spectroscopy (XRF) Cu, Cd, Cr, and V were below the detection limits of the instrument (<3.0 ppm), Ni was found at levels averaging 2.0 ppm, and Fe, Zn, and Ba levels were below 10 ppm in the four species studied (J.M. Kalish, unpubl. data). Edmonds et al. (1989) used inductively coupled plasma atomic-emission spectroscopy (ICP—AES) to study otolith composition of the pink snapper *Chrysophrys auratus* for stock discrimination, and their data indicate that Mg, Si, and Fe are at levels below the detection limits achievable using either ED or WD microprobe analysis.

With the above results in mind it appears that with a WD electron microprobe the only elements that can be reliably quantified in otoliths are Ca, Na, Sr, K, S and, in some cases, Cl. However, in the case of Cl, the presence of this element in the most frequently used mounting medium, epoxy, makes the quantitative determination of this element difficult. If it is desired to detect Cl, an alternative mounting medium should be considered. The utility of ED microprobe analysis to studies of the quantitative composition of fish otoliths seems to be limited to Ca and, in some rare instances, Na and Sr.

Although WD microprobe analysis is generally capable of detecting the levels of Sr found in freshwater and marine fish otoliths, there are some limitations to the method in studies of anadromous fishes. Most important is the limited spatial resolution of the microprobe. In this study the probe size was maintained at 10×10 μm to minimize beam damage of the specimen. A spot of this size on the otolith of an adult fish would encompass more than a single day of otolith growth and in slow-growing individuals could encompass a month or more. In slow-growing fish, this would limit the ability to determine the temporal scale of migratory events. Determination of the temporal resolution of the microprobe data would be dependent on estimates of fish age based on otolith annuli and microincrement data. In many instances, the utility of otolith Sr data is dependent on the accurate determination of age using the same otolith.

The elemental analysis of otolith primordia should provide an objective criterion for assessing if an individual is the progeny of an anadromous or non-anadromous female. This information alone, or in combination with data from life-history transects, should make it possible to investigate the relationships between genetics and environment on diadromous behavior and aid in the management of species that display faculative diadromy. However, as with any new method, it is important to confirm the validity of these results for the particular species and habitat in question.

Acknowledgments

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Comparison Between Fish Bycatch from Shrimp Trawlnet and Visual Censuses in St. Vincent Bay, New Caledonia

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Abstract.—Density and biomass estimates from a shrimp trawl and a visual survey are compared. Results indicate that the visual survey gives estimates eight to nine times larger than the trawl survey. However, there are important variations by species. Estimates of fish size from the visual censuses are larger than fish sizes observed in the trawl catch. These results suggest that the catchability of fish by shrimp trawls may be lower than usually thought for multispecies tropical stocks. In shrimp trawl fisheries, this may have important consequences for stock assessment and for evaluation of parameters such as fishing mortality. Trawling should be adequate for qualitative and semiquantitative stock assessment, but will need to be compared with other methods for quantitative studies on multispecific stocks.

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Shrimp trawl fisheries are the source of a large fish bycatch in the tropical Indo-Pacific (Aoyama 1973, Grantham 1980, Villoso and Hermosa 1982, Chong 1984). One question concerning these fisheries is how much damage they cause to fish stocks. To answer this question, it is useful to assess the catchability of fish by shrimp trawls. Many methods exist to assess this parameter. Most use the same gear under different conditions, such as double codends, split codends, and replicate hauls with different mesh sizes (Macket 1973, Gulland 1975). The bias of such methods may be acceptable for single-species populations but has seldom been studied in relation to tropical multispecies stocks. Another approach is the cross-evaluation of trawling and echosurveys (Doubleday 1976, Dines 1982, Dickie et al. 1983), but this method is not well adapted to tropical multispecies stocks. Another way is to correlate the results of two methods, such as with a TV camera and otter trawl (Uzmann et al. 1977), submersible and longlines (Ralston et al. 1986, Richards and Schnute 1986, Grimes et al. 1982), visual census and longlines (Kulbicki 1988) or poisoning and beamtrawl (Gray and Bell 1986).

The use of several methods has the advantage of allowing some evaluation of the biases of each method. In the present study it was possible to compare the results of visual censuses and shrimp trawl bycatches. This work was originally designed to estimate the catchability of the net (q = number of fish caught/number of fish present), but it also provided information on the biology of the fish.

Material and methods

Location

The study was performed during August 1986 on the trawling grounds of the South Bay in St. Vincent Bay, in the southwest lagoon of New Caledonia. The trawling grounds cover 15 km^2, or approximatively one-tenth of the Bay area. A total of eight stations were sampled (Fig. 1), one of which was sampled at night (Station n°6).

Visual census

A 200-m transect line was laid on the bottom with a buoy set at each end of the line. The transect was divided into 10-m sections. For each section, two divers—one on each side of the line—counted all fish, estimated their length, and estimated the perpendicular distance of the fish to the transect. Length was given in 2-cm size classes for fish less than 20 cm, 5-cm size classes for fish between 20 and 50 cm, and 10-cm size classes for fish larger than 50 cm. Only fish less than 1.5 m above the bottom were counted. The distance from the fish to the transect was recorded in 1-m

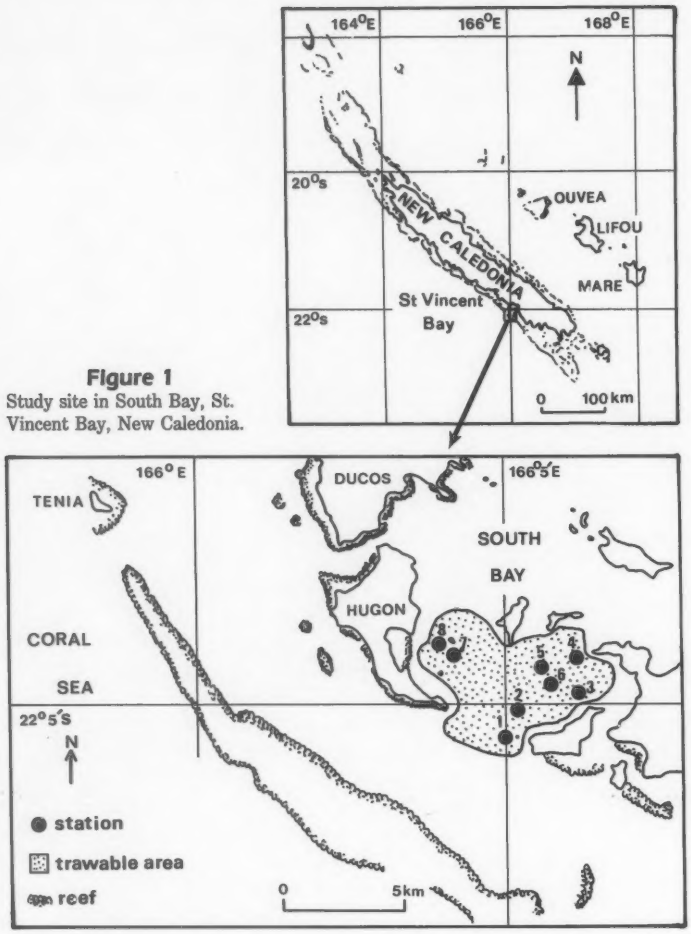

Figure 1
Study site in South Bay, St. Vincent Bay, New Caledonia.

classes up to 5 m, and in 2-m classes beyond 5 m. Fish were not recorded beyond 10 m from the transect. Both divers had a good knowledge of the fish fauna and also had a good training in visual censuses. The transects were finished between 30 and 45 minutes before the start of the trawling.

For this type of data, many density estimators may be chosen (Burnham et al. 1980). Among these estimators, Kulbicki and Duflo (unpubl. data) show that the most robust one for fish density (D) in similar conditions is given by:

$$D = (10^4/2L) \sum_{i=1}^{p} (n_i/d_i)$$

where D = fish density (fish/ha),
p = number of species,
n_i = number of fish of species i,
d_i = average distance (m) of species i to the transect, and
L = length of the transect (200 m).

Biomass B (kg/ha) was calculated in a similar fashion:

$$B = (10/2L) \sum_{i=1}^{p} (w_i/d_i)$$

where w_i = weight of species i (g).

The weights of fish were estimated from length-weight relationships (Wantiez and Kulbicki In press).

Trawling

The RV *Vauban* (24 m long) towed a shrimp trawlnet of the semiballoon, floridian type with a 14-m headrope and a 2-cm mesh codend. The vertical opening was 1.2 m and the distance between the otterboards was 7 m at a speed of 2 knots. Towing speed varied from 2 to 2.5 knots.

The hauls were each 800 m in length (±80 m). The net was submerged immediately after completion of the visual census at a distance of 400 m from the first buoy of the transect. The track of the haul was along the transect line and the net was retrieved 200 m after the second buoy of the transect line. All fish caught were sorted to species (Rivaton et al. 1990). All fish were counted and weighed.

For the calculation of density D (fish/ha), no catchability coefficient was used. Therefore,

$$D = \sum_{i=1}^{p} (n_i/S)$$

where p = number of species caught,
n_i = number of fish of species i, and
S = surface area of the haul (7 m × 800 m = 5600 m^2 = 0.56 ha).

Biomass (kg/ha) B was estimated in a similar fashion,

$$B = \sum_{i=1}^{p} w_i/S)$$

where w_i = weight of species i (kg).

Results

Species

A total of 82 species were either caught by trawls or recorded by divers (Table 1). All the common species known to occur in trawls in St. Vincent Bay (Kulbicki and Wantiez 1990) were found in the present study except for the Leiognathidae (ponyfishes). This family, represented by eight species in the bay, is characterized by large fluctuations in trawl catches depending on season and locality. In the present survey, *Leiognathus rivulatus* which is normally an uncommon species in the catch, was the major Leiognathidae.

Table 1 indicates that the trawls caught more species (64) than were seen on the transects (51). This could be due to the larger area covered by the trawls (~5600 m^2/trawl versus 700–1000 m^2 per transect). Most cryptic species, such as Scorpaeniforms, Platycephalidae (flatheads), flatfishes, and small Balistidae (triggerfishes) (including the filfishes *Paramonacanthus japonicus* and *Pseudalutarius nasicornis*) were poorly represented in the visual transects but caught by the trawls. Conversely, small species such as Apogonidae (cardinalfishes) and Pomacentridae (damselfishes) could be detected on the transects but were too small to be retained by the net. Large, fast-swimming species such as Carangidae, Serranidae, or Scombridae were seen on the transects but evaded the trawls. Gobiidae, which are burrowing species, were also seen during the dives but absent from the trawl catch.

A total of 32 species were detected by both methods (Table 1). Among these, only eight species were seen or caught in more than 50% of the samples for both methods (*Saurida undosquamis*, *Synodus hoshinonis*, *Leiognathus rivulatus*, *Lethrinus nematacanthus*, *Upeneus tragula*, *Upeneus* sp. aff. *asymetricus*, *Pristotis jerdoni*, and *Canthigaster compressa*). These eight species will subsequently be referred to as "main species." Except for *Synodus hoshinonis* and *Leiognathus rivulatus*, all these fish are among the 15 most frequent species in the trawl catch of St. Vincent Bay (Kulbicki and Wantiez 1990).

The number of species per station was statistically larger (t test at $\alpha = 0.05$) for the trawls than for the transects (Table 2). However, a chi-square test for independent samples (Siegel and Castellan 1988) indicates that the ranking of the stations is not significantly different (at $\alpha = 0.05$) between methods.

Fish size

Only fish lengths were used to compare fish size between the two methods. Table 3 indicates that visual censuses always yielded larger lengths than trawls, except in the case of *Pristotis jerdoni*. However, the lengths are significantly different (t test at $\alpha = 0.05$) for only four species (Table 3), and the two methods give mean lengths which are less than 2.8 cm apart. Due to the fact that fish length was estimated in 2-cm size classes for transects and 0.5-cm size classes for trawls, one should be cautious about the significance of the differences observed.

In a review on the problems of visual transects, Harmelin-Vivien et al. (1985) indicate that fish size is usually underestimated by this method. In the present study, if this were the case, it would mean that the larger fish (within a given species) are able to evade the trawl. In our opinion this is not the only reason, and the discrepancy of fish length between transects and trawls is probably also due to an overestimate of length by the divers.

Table 1

Species composition of transects and trawls in St. Vincent Bay, New Caledonia. For dives and trawls, numbers indicate at how many stations the species were recorded.

Species	Dives	Trawls
Muraenidae		
Muraenidae spp.	1	4
Synodontidae		
Saurida gracilis	0	2
Saurida nebulosa	0	2
Saurida undosquamis	4	4
Synodus dermatogenis	1	0
Synodus hoshinonis	4	7
Trachynocephalus myops	0	1
Carapidae		
Carapus homei	0	1
Fistularidae		
Fistularia petimba	0	1
Syngnathidae		
Hippocampus histrix	0	1
Dactylopteridae		
Dactyloptena orientalis	0	2
Scorpenidae		
Scorpaenidae sp.	0	1
Dendrochirus brachypterus	0	1
Pterois volitans	1	0
Synanceiidae		
Inimicus didactylus	0	3
Aploactinidae		
Aploactis aspera	0	2
Platycephalidae		
Platycephalidae spp.	1	7
Onigocia spinosa	0	3
Serranidae		
Cephalopholis boenack	2	0
Epinephelus cyanopodus	2	0
Epinephelus maculatus	3	0
Epinephelus malabaricus	0	1
Priacanthidae		
Priacanthus hamrur	0	2
Apogonidae		
Apogon spp.	2	1
Apogon catalai	0	1
Apogon ellioti	0	4
Apogon aureus	1	0
Apogon frenatus	1	1
Apogon sp. cf *compressus*	0	1
Cheilodipterus quinquelineatus	0	1
Rhabdamia spp.	1	0
Carangidae		
Decapterus russeli	1	2
Gnathanodon speciosus	1	0
Siganidae		
Siganus canaliculatus	0	3
Scombridae		
Scomberomorus commersoni	1	0
Bothidae		
Arnoglossus sp.	0	1
Asterorhombus intermedius	1	8
Engyprosopon grandisquama	1	7
Grammatobothus polyophthalmus	0	3
Balistidae		
Abalistes stellatus	0	3
Paramonacanthus japonicus	1	7
Pseudalutarius nasicornis	2	4
Leiognathidae		
Leiognathus rivulatus	5	6
Secutor ruconius	1	0
Lutjanidae		
Lutjanus quinquelineatus	2	2
Lutjanus vittus	2	3
Gerreidae		
Gerres ovatus	1	3
Haemulidae		
Diagramma pictum	2	1
Lethrinidae		
Lethrinus nematacanthus	6	8
Lethrinus semicinctus	1	2
Nemipteridae		
Nemipterus peroni	0	2
Scolopsis temporalis	3	6
Mullidae		
Parupeneus pleurospilos	1	4
Upeneus sp.	0	1
Upeneus moluccensis	1	2
Upeneus tragula	7	7
Upeneus sp. aff. *asymetricus*	6	8
Chaetodontidae		
Heniochus acuminatus	1	1
Pomacentridae		
Chromis fumea	1	0
Dascillus aruanus	0	1
Neopomacentrus sp. Allen	1	0
Pristotis jerdoni	4	5
Labridae		
Anampses spp.	1	0
Cheilinus bimaculatus	2	6
Xiphocheilus typus	0	2
Scaridae		
Scarus ghobban	0	1
Mugiloididae		
Parapercis sp.	2	0
Parapercis cylindrica	4	2
Blenniidae		
Petroscirtes breviceps	2	4
Callionymidae		
Synchiropus rameus	0	2
Gobiidae		
Gobiidae sp.	2	0
Amblyeleotris sp.	2	0
Amblygobius sp.	1	0
Pterleotris hanae	1	0
Ostraciidae		
Tetrasoma gibbosus	0	5
Lactoria cornuta	0	3
Tetraodontidae		
Amblyrhynchotes hypselogeneion	0	3
Arothron immaculatus	3	6
Arothron stellatus	1	3
Canthigaster compressa	8	8
Canthigaster valentini	2	0
Lagocephalus sceleratus	1	1
Total number of species	51	64
Species common to both methods	32	
All species	82	

Table 2

Number of species per station according to transects and trawls, St. Vincent Bay, New Caledonia. CI = confidence interval at $\alpha = 0.05$.

	Station number									
	1	2	3	4	5	6	7	8	Average	CI
Transects	13	11	18	4	16	16	14	15	13.4	9.5–17.2
Trawl	22	31	25	18	20	38	21	27	25.3	19.3–31.2

Chi-square value for two independent samples = 7.63. Limit value = 14.07 (7 df) at $\alpha = 0.05$ (Siegel and Castellan 1988).
Station 6 was performed at night.

Table 3

Comparison of fish lengths given by transects and trawling for main species, St. Vincent Bay, New Caledonia.

	Trawl			Transect				
Species	L	n	$s/\sqrt{n}$	L	n	$s/\sqrt{n}$	F	t
Saurida undosquamis	22.7	108	0.07	23.3	8	1.10	**	0.50 NS
Platycephalus sp.	14.6	12	0.29	15.0	1		—	—
Leiognathus rivulatus	8.2	130	0.07	9.2	499	0.41	—	1.30 NS
Lethrinus nematacanthus	12.2	186	0.12	14.3	244	0.08	—	14.9 **
Scolopsis temporalis	14.0	22	0.58	14.8	4	0.25	**	1.16 NS
Upeneus tragula	12.0	26	0.60	14.8	30	0.55	NS	3.46 **
Upeneus sp. aff. *asymetricus*	10.9	329	0.07	12.0	46	0.20	—	5.52 **
Pristotis jerdoni	9.1	46	0.08	8.7	490	0.04	—	4.92 **
Paramonacanthus japonicus	9.0	30	0.13	10.0	1		—	—
Pseudalutarius nasicornis	11.3	3	0.83	12.6	5	1.12	—	0.78 NS
Canthigaster compressa	8.3	217	0.06	8.6	38	0.20	—	1.62 NS

L = length in cm,
n = sample size,
$s/\sqrt{n}$ = standard error,
F = Fmax test for homogeneity of variance (Sokal and Rohlf 1981) performed if $n<30$,
t = Student test if F not significant, otherwise t' test for samples of unequal variance (Sokal and Rohlf 1981),
** = significant at $\alpha = 0.01$,
NS = not significant at $\alpha = 0.05$, dashes indicate not calculated.

Abundance and biomass

Density estimates from transects were on average 9.7 times larger than from trawls, this difference being highly significant (F test for paired comparison (Sokal and Rohlf 1981) at $\alpha = 0.01$) (Table 4). Depending on the species, the ratio between the two methods varied from 0.9 to 80 (Table 5). If one considers only the eight most common species mentioned in the previous section, then the ratio is 7.93. This would indicate a catchability of the trawl net of 0.103 for all species and 0.127 for the main species. Species for which the ratio is close to 1 (Synodontidae, *Canthigaster compressa*, *Upeneus* spp.) are difficult to detect underwater. This can be due to either their behavior (e.g., Synodontidae are usually motionless on the bottom, and at times, half buried in the sand) or to their coloration (*Canthigaster compressa* being well camouflaged among algae, and *Upeneus* spp. being able to drastically change their coloration to mimic the bottom). In addition, Table 6 indicates that these criptic species are usually found singly or in pairs.

Species with a high ratio (Apogonidae, *Leiognathus rivulatus*, *Pristotis jerdoni*) are not caught by the net for two main reasons. Either they are too small (Apogonidae, most *Pristotis jerdoni*) or they swim too high above the bottom (*Leiognathus rivulatus* were usually 0.5–3 m above the bottom) for the net to catch them. These fish are also found in small schools (21–36 fish/sighting) (Table 6). The correlation between the two methods (Table 5) is some indication of the patchiness of the distribution of these species. Thus a high correlation such as for the Synodontidae ($r = 0.75$) or *Leiognathus rivulatus* ($r = 0.92$), indicates that these

Table 4

Density estimates (fish/ha) for all species for visual transects and trawls, St. Vincent Bay, New Caledonia. CI = confidence interval ($\alpha = 0.05$).

	Station number									
	1	2	3	4	5	6	7	8	Average	CI
Transect	6020	7190	1930	8650	2610	1160	1750	4340	4200	1690–6700
Trawl	245	620	183	312	590	920	197	380	431	200–662

F test value for paired comparison = 15.1. Limit value = 5.59 (1, 7 df) at $\alpha = 0.05$.

Table 5

Comparison of density and biomass estimates from transects and trawls for main families and species, St. Vincent Bay, New Caledonia.

Family or species	Density		Biomass	
	ratio	r	ratio	r
Synodontidae	0.88	0.75*	0.80	0.93**
Apogonidae	80	0.66	13	0.78*
Leiognathus rivulatus	33	0.92**	49	0.97**
Lethrinus nematacanthus	7.4	−0.03	10	−0.02
Upeneus spp.	2.3	0.63	4	0.57
Pristotis jerdoni	29	0.04	39	0.03
Canthigaster compressa	1.2	0.49	1.3	0.40
All species	9.7	−0.17	9.1	0.72′
Main species (see text)	7.9	0.23	6.4	0.34′

Ratio = density from transects/density from trawls,
r = correlation coefficient,
* significant at $\alpha < 0.05$, ** significant at $\alpha < 0.01$.
′ night station (n°6) not included.

Table 6

Average distance between sightings and number of fish per sighting for main families and species, St. Vincent Bay, New Caledonia.

Family or species	Average distance between sightings (m)	Number of fish per sighting
Synodontidae	110	1
Apogonidae	260	35
Leiognathus rivulatus	120	36
Lethrinus nematacanthus	28	4
Upeneus spp.	35	1.8
Pristotis jerdoni	80	21
Canthigaster compressa	55	1.3

species are rather uniformaly distributed on the bottom. Conversely, species such as *Lethrinus nematacanthus* ($r = 0.03$) or *Pristotis jerdoni* ($r = 0.04$) have a very patchy distribution. A pratical consequence is that a larger number of stations will be needed to get a good stock assessment for the latter species than for the former.

Biomass estimates from transects are 9.1 times larger than those from the trawls (Table 7), this difference being significant (F test for paired comparison (Sokal and Rohlf 1981) at $\alpha = 0.05$). Although density estimates for all species were not correlated between trawls and transects ($r = -0.17$), biomass estimates show some correlation between the two methods, if the night station n°6 is excluded ($r = 0.72$, significant at $\alpha = 0.07$). The absence of correlation between the two methods in the density estimates may be explained by the large contribution of small fish such as Pomacentridae to transect density estimates, whereas these species escape the net. Conversely, biomass estimates are almost unaffected by these species because of their small weight. At the species level the correlations between the two methods for biomass estimates are of the same magnitude as those observed for density estimates.

Discussion

The comparison of two methods with such different concepts requires some adjustments. Trawls swept approximately 5600 m^2 and transects covered between 700 and 1000 m^2 (depending on species) for each station. The trawls did fish over the transect lines, but a perfect match would mean a trawl track with a precision of ±1 m which is untractable even in shallow water. This is, in our opinion, the main source of difference in the number of species given by each method.

Table 7

Biomass estimates (kg/ha) for transects and trawls, St. Vincent Bay, New Caledonia. CI = confidence interval at $\alpha = 0.05$.

	Station number									
	1	2	3	4	5	6	7	8	Average	CI
Transect	225	242	49	65	160	43	123	74	123	53–193
Trawl	10	19	8.3	4.9	11	34	15	6	13.5	5.0–22.0

F test value for paired comparison = 15.0. Limit value is 5.59 (1, 7 df) at $\alpha = 0.05$ (Sokal and Rohlf 1981).

Because of the low number of stations, this difference in sampled area may also be important to explain the low correlation between the two methods for density or biomass estimates of fish with a patchy distribution. Conversely, comparisons of the density or biomass for fishes with a regular distribution should not be affected.

An important result from the present survey is the magnitude of the difference between trawl and transect estimates of density. This difference, which is a factor of 9.7 for all species and a factor of 7.9 for the main species, certainly indicates that shrimp trawls poorly sample the bottom fish fauna in St. Vincent Bay. Visual transects are usually performed as strip transects, where distance of the fish to the transect line is not taken into account (Harmelin-Vivien et al. 1985). This underestimates density, especially if the width chosen is large (Burnham et al. 1980). The method chosen in the present survey is more accurate; however, it is not possible to know by how much one underestimates or overestimates the "real" density. Fish numbers (Harmelin-Vivien et al. 1985) and distances are both underestimated but play opposite roles in the density estimation. Even in the unlikely case of a large overestimate of fish density (let's suppose by 100%) by transects, the catchability of the trawl would still be 0.25 for the main species and 0.21 for all species.

Several surveys indicate that trawls may not be as efficient as usually thought. Thus Uzmann et al. (1977) found that estimates of fish density from submersibles were 8.0 times greater than density estimates from otter trawls, this ratio varying between 0.8 and 18 depending on the species. Similarly, Gray and Bell (1986) found that poisoning indicated densities 2.5 to 6.5 times greater than a beam trawl over seagrass beds. However, in some conditions trawling may be more efficient, as shown by Harden Jones et al. (1977) who used accoustical tags to estimate that 44% of the tagged flatfishes *Pleuronectes platessa* were caught by a Granton otter trawl. Uzmann et al. (1977) had found that only 7% of the flatfishes seen from a submersible were caught by the otter trawl. Serebrov (1986) used submersibles to show that the catchability of an otter trawl varied with the size of the fish, mesh size, and overall catch composition.

In the case of one or a few species, catchability of trawls may vary between 0.5 and 1.0. Such values of catchability are widely used, even in multispecies tropical fisheries, for which Pauly (1982) states that a value of 0.5 is "realistic" and Gulland (1979) even suggests that a catchability of 1.0 should apply to the eastern Indian Ocean trawl fisheries. In many of these fisheries, shrimp trawls of design similar to the one used in the present experiment are used to get a mixed catch of shrimp and fish (Grantham 1980, Poiner and Harris 1986, Lamboeuf 1987, Sainsbury 1987). Our results indicate a catchability near 0.1 (0.103 for all species and 0.127 for the main species). Such a value may need further testing; but if it proved correct, it would have important implications in the management of these tropical multispecies trawl fisheries. In particular, depending on whether one uses a catchability of 1.0 or 0.1, stock size will increase by a factor of 10. This would also affect the estimated fishing mortality (Pauly 1982) and, as a result, most of the equations used in stock management. What is more important, in our opinion, is that if one applied a catchability of 0.1 in most of these tropical trawl fisheries of the Indo-Pacific, the current models would be unable to explain the long-term decline of the catch seen in these fisheries. This could mean that trawling induces detrimental changes in fish populations which are beyond the simple removal of fish. In particular, habitat changes may be important, as noted by Poiner and Harris (1986) and Sainsbury (1987).

Another question arising from the present work is the value of the catch per unit effort (CPUE) of trawls as an indicator of population abundance. Our results show a poor correlation between abundance estimates from trawls and visual transects at the population level, but good correlations for a few selected species. Numerous studies have examined the correlation of CPUE by trawling and acoustic surveys. Most of these indicate good correlations (see Tesler (1977), Olsen et al. (1977), or Thorne (1977a) among others) but important varia-

tions may result from fish behavior (Thorne 1977b). However, most of these surveys are performed on a single pelagic or semipelagic species, and the correlation between acoustic surveys and CPUE by trawling for multispecies tropical stocks is currently poorly documented. Soetre and Paula e Silva (1979) found from comparison between demersal trawl catch and echointegration on a multispecific stock off Mozambique that the catchability of the otter trawl was 0.3. These authors state that this value is "suspiciously low for demersal species." Guillory et al. (1982) concluded from replicate sampling with otter trawls that this type of gear should be used strictly for qualitative purposes in a multispecies situation. This is in part supported by the present work, which indicates a need for alternate methods of stock assessment. Longlines show similar problems to trawling. Thus, correlation between longline CPUE and observed densities from a submersible was weak at the multispecies level (Richards and Schnute 1986, Ralston et al. 1986) but satisfactory for some selected species. Similar work involving longline CPUE and observed densities by visual transects indicated a good correlation for all species ($r = 0.88$) but considerable variations depending on species (Kulbicki 1988). Visual census either by diving or from submersible might be an alternative, but these methods also have numerous limitations. In particular, they do not allow a quick coverage of large areas and are not usable in turbid waters. If reasonably accurate density estimates are required in a multispecies tropical trawl fishery, it is likely that this can be achieved only by a combination of several independent methods.

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Food Availability as a Limiting Factor to Mussel *Mytilus edulis* Growth in California Coastal Waters

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Abstract.—Relationships between mussel shell growth and environmental parameters were investigated in the mussel *Mytilus edulis* at an inshore location, Avila Beach, and at an offshore location, oil platform Holly (ARCO). Temporal patterns of mussel growth were similar at both locations. Mussel growth rate was related to chlorophyll *a* concentration at Holly, but not at Avila. Theoretical estimates of scope for growth (SFG) were made for mussels at each location using published physiological data. Good agreement was found, with a time lag, between estimated SFG and shell growth. The SFG analysis independently supported the conclusion that temporal changes in phytoplankton concentration limits mussel growth at Holly, but suggested that changes in the composition, rather than the concentration, of suspended particulates limits growth at Avila, as reported for mussels in estuarine environments.

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Temporal variability in growth rate has been extensively documented for many species of filter-feeding marine invertebrates. Growth rates frequently vary "seasonally," with most rapid growth occurring during the spring and summer months. Season is an ambiguous concept, however, which does not satisfactorily describe factors regulating temporal patterns of growth. Ultimately, environmental factors, which vary over time and with location, contribute to variation in growth rates. The growth rate of mussels *Mytilus edulis* varies in both time and space. Mussel growth rates near Santa Barbara, California, are highest from May through August (Harger 1970; Page and Hubbard 1987), but elevated rates can also occur during the winter months (Page and Hubbard 1987). Physiological and ecological evidence indicates that in many situations worldwide, food availability may be the most important single factor regulating mussel growth (Seed 1976, Widdows et al. 1979, Incze et al. 1980, Rodhouse et al. 1984). Multiple regression and correlation analysis indicated that mussel growth rate was associated with phytoplankton abundance, but not water temperature, at an offshore location in the Santa Barbara Channel (Page and Hubbard 1987).

Variation in the concentration and composition of phytoplankton and other suspended particulates which could influence mussel growth exists in the open coastal environment. For example, episodic upwelling and high primary productivity characterize the region north of Point Conception, California, relative to the Santa Barbara Channel (Owen 1980, Willason et al. 1986). Inshore areas tend to be more productive and to possess higher total seston concentrations than offshore areas, and phytoplankton concentration varies with depth (Raymont 1980). Little information is available regarding spatial relationships between phytoplankton abundance and mussel growth in inshore waters.

In this study, we used correlation analysis and the "scope for growth" concept to evaluate the potential importance of temporal and spatial variation in food availability to mussel growth. The concept of scope for growth (SFG, Warren and Davis 1967), as applied to mussels, has been reviewed by Bayne et al. (1976a) and Widdows (1985a). SFG analysis uses physiological relationships, together with environmental parameters, to estimate the potential production of soft tissue (soma and gonad) by mussels from the general energy equation, $SFG = A - (R + U)$, where SFG = energy available for growth of soft tissue, A = energy absorbed from food, R = respiratory heat loss, and U = energy lost as excreta. Radford and Bayne (cited in Bayne et al. 1976a) and Radford et al. (1981) successfully used this concept to model

mussel growth in British waters. SFG analysis may thus prove useful in interpreting relationships between mussel growth and environmental factors in California waters.

The present study, which continued work reported in Page and Hubbard (1987), (1) compared mussel growth rates in highly productive inshore coastal waters north of Point Conception with rates measured concurrently at offshore Platform Holly (Atlantic Richfield Company), (2) evaluated the relationship between temporal and spatial variation in growth and measurements of potential food availability, and (3) used published physiological data and the "scope for growth" concept (Bayne et al. 1976a) to provide an independent assessment of the response of mussel growth to environmental conditions in California waters.

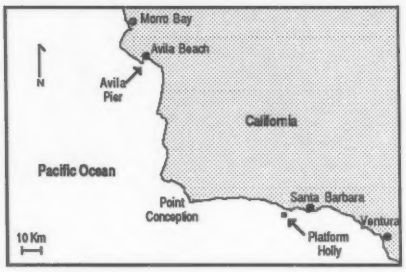

Figure 1
Locations of the Avila Beach and Platform Holly study sites.

Materials and methods

Study sites

Avila Beach (35°10′N, 120°43′W) is located approximately 84 km north of Point Conception, California (Fig. 1), in a region characterized by episodic upwelling and high primary productivity (Owen 1974, 1980; Lasker et al. 1981). The study site was located at the end of the Unocal pier which extended 0.8 km into semiprotected Avila Bay. Water depth at this location was about 12 m. *Mytilus edulis* were collected intertidally on pier pilings, since subtidal mussels were scarce due possibly to starfish predation (Landenberger 1967).

Platform Holly is a 20-year-old oil and gas production platform located in 60 m of water, about 3 km offshore of Goleta, California (34°25′N, 119°52′W; Fig. 1). Mussels colonize the support members of this platform from the intertidal zone to depths greater than 18 m, and grow rapidly, achieving 50 mm shell-length in 6–8 months (Page and Hubbard 1987).

Physical and biological parameters

We collected water samples at a depth of 2 m with a Van Doren bottle every 7–10 days at each location from October 1986 to June 1987. Temperature of samples was measured by hand-held thermometer. Estimates of potential food available to mussels were made from the concentrations of seston, particulate organic matter (POM), chlorophyll *a* (an estimate of phytoplankton biomass: Lorenzen 1970, Hunter and Laws 1981), and particulate organic carbon (POC) in replicate 500-mL water samples. All water samples were prefiltered through a 300-μm nylon mesh. Seston concentration was measured using standard methods (Widdows 1985b). Percent of POM (% POM) within the seston was calculated as 100 · [POM]/[seston]. Chlorophyll *a* concentration was determined using standard fluorometric methods (Parsons et al. 1984) and a Turner Designs Fluorometer. Particulate organic carbon concentration was determined using a Perkin-Elmer CHN analyzer following the methods of Rodhouse et al. (1984).

Growth rate of *Mytilus edulis*

Twenty individually numbered mussels (~20 mm shell-length), collected intertidally (~ – 15 cm), were enclosed in a cylindrical vexar plastic cage (12 × 20 cm, 5-mm mesh) monthly at each site from November 1986 to June 1987. Using calipers, shell-lengths of caged mussels were measured to the nearest 0.1 mm initially and after 4 weeks. No growth data are available at Avila from January and February 1987, due to lack of small mussels. Cages were submerged at depth (– 2 m) either by suspension on a weighted line (Holly) or by attachment to a pole (Avila). Cages were cleaned as needed to keep fouling to a minimum.

Transplant experiments

We conducted transplant experiments in Fall 1986 to evaluate the potential influence of mussel stock on growth rate. Forty *M. edulis* were collected from Holly on 27 September 1986 and transplanted (2 cages of 20 individuals of ~30 mm shell length) to Avila on 29 September 1986. Mussels of equal size and number were collected from Avila on 29 September 1986 and transplanted to Holly on 4 October 1986. Mussels were covered with a moist cloth in transport and maintained in unfiltered seawater prior to placement in the field.

Mention of trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Physiological parameters and relationships used in SFG analysis of *Mytilus edulis*. W = soft tissue dry wt. (g), L = shell length (mm), [seston] = seston concentration (mg/L), T° = water temperature (°C).

Physiological parameter	Regulatory factor(s)	Comments	Relationship	Source
1) Clearance rate (CR, L/h)	W [seston]	Independent of temperature (a, b, c). ANCOVA adjusted common slope and mean of intercepts of CR vs. W curves from (a) combined with median slope of CR vs. [seston] relationship for three size classes in (b).	$CR = 1.73 \cdot W^{0.413} - 0.006 \cdot [seston]$ if $CR < 0.1$ L/h, then $CR = 0.1$ L/h	a) Thompson 1984 b) Widdows et al. 1979 c) Widdows 1978
2) Seston filtered (SF, mg/h)	CR [seston]	Assume 100% retention efficiency.	$SF = CR \cdot [seston]$	
3a) Pseudofeces threshold (T, mg/L)	W	Shape of pseudofeces vs. food concentration curve of (d) combined with size-specific threshold values measured by (b). Technique alluded to in (e).	$T = 3.81 \cdot \log L - 1.93$	d) Foster-Smith 1975 b) Widdows et al. 1979 e) Bayne and Worrall 1980
3b) %Pseudofeces (%Ps)	T [seston]		$\%Ps = 100 - [(86.4\ e^{0.288\ T}) \cdot [seston]^{-(0.489T^{0.329})}]$	
4) Seston ingested (SI, mg/h)	SF %Ps		$SI = SF - (SF \cdot \%Ps/100)$	
5) Absorption efficiency (AE)	%POM	Model of (f).	$AE = 0.5 \cdot \log(\%POM) - 0.32$	f) Bayne et al. 1979
6) POM absorbed (A, mg/h)	SI AE		$A = (SI \cdot \%POM/100) \cdot (AE/100)$	
7) Respiratory rate (VO_2, mLO_2/h)	W T°	b value determined from average of all monthly regressions in (a). Temperature effect described by exponential curve fitted to data from (a) and (g). VO_2 considered independent of ration at [seston] >2 mg/L.	$VO_2 = a \cdot W^b$ $b = 0.782$ $a = 0.117 \cdot (10^{0.044\ T°})$	a) Thompson 1984 g) Widdows et al. 1984
8) Scope for growth (SFG, J/h)	A VO_2		$SFG = (A \cdot 23.5) - (VO_2 \cdot 20.3)$	

Growth rates of transplanted individuals were compared with that of 40 resident individuals enclosed in cages (2 cages of 20 individuals of ~30 mm shell length) and submerged at the same time.

Scope for growth

Relevant physiological parameters, regulatory factors, and relationships used in our analysis of SFG are given in Table 1. Environmental parameters required to estimate SFG (water temperature, seston concentration, and %POM) were measured in this study, while physiological relationships were derived from information in the literature.

Absorbed food was estimated from measurements of mussel size, seston concentration, %POM, and from published values for size-specific clearance rate, ingestion rate and absorption efficiency. Whenever possible, we used data on clearance and ingestion rates and

absorption efficiences obtained using "natural" POM. Clearance and ingestion rates of particulate material were assumed to be independent of water temperature, but dependent on mussel size and particle concentration (Foster-Smith 1975, Bayne et al. 1976b, Widdows 1978, Widdows et al. 1979). The fraction of filtered seston rejected as pseudofeces (% pseudofeces, Table 1) was determined from ingestion rate and the critical POM concentration (3.0 mg/L for a 20-mm mussel; Widdows et al. 1979). The percent pseudofeces represents the fraction of filtered seston rejected as pseudofeces. Absorption efficiency was estimated using the model of Bayne et al. (1979; Table 1). The caloric content of the absorbed food was assumed to be 23.5 Joules/mg dry POM (Widdows 1985b).

Metabolic expenditures were estimated given mussel size, water temperature, and published data on oxygen consumption (Thompson 1984, Widdows et al. 1984; Table 1). Published oxygen consumption measurements were converted to an energetic equivalent of 20.3 Joules/mL O_2 (Crisp 1971). Energy losses due to excretion are generally minor (as a percent of absorbed ration: 4.3–5.9%, Bayne et al. 1979; 1.7–4.3%, Widdows et al. 1980; 0.4–2.0%, Thompson 1984; 0.5–2.9%, Widdows and Shick 1985) and were ignored here. SFG (Joules/hour) was estimated as (absorbed POM, mg/hour × 23.5 J/mg) − (mL O_2/hour × 20.3 J/mL O_2).

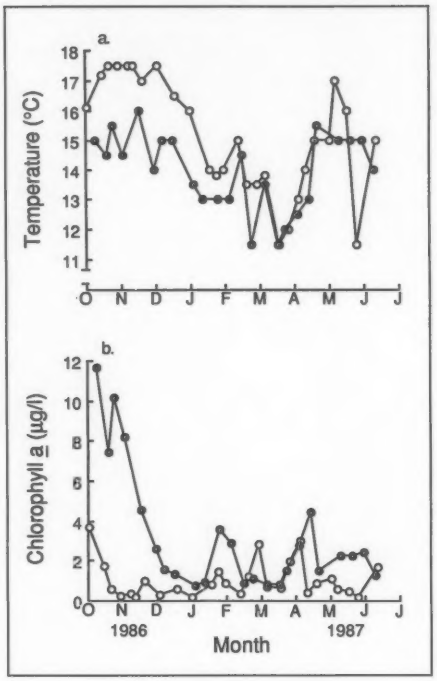

Figure 2
(a) Water temperatures and (b) chlorophyll *a* concentrations at Avila Beach (●) and Platform Holly (○).

Results

Physical and biological parameters

Surface water temperature was significantly lower at Avila than at Holly ($t = 2.46$, df = 49, $P<0.01$, Student's t-test; Fig. 2a). Water temperatures at Avila were up to 3°C cooler than at Holly from October through December 1986.

Surface chlorophyll *a* concentration was significantly higher at Avila than at Holly ($t = 3.53$, df = 49, $P<0.001$, Student's t-test; Fig. 2b). Chlorophyll *a* concentrations were as much as 20 times higher at Avila than at Holly from October through November 1986.

Seston concentration was higher at Avila than at Holly ($t = 3.88$, df = 46, $P<0.001$; Fig. 3a). The highest values at Avila (10–30 mg/L) January through February coincided with seasonal storms. Seston levels remained low at Holly, fluctuating between 1 and 5 mg/L during most of the year.

Particulate organic matter concentration was higher at Avila than at Holly ($t = 2.04$, df = 40, $P<0.05$; Fig. 3b). Particulate organic matter concentrations at Avila generally varied between 1 and 5 mg/L, but reached 10 mg/L in January 1987. Particulate organic matter concentrations at Holly ranged from <0.5 mg/L to a high value of 4 mg/L during a phytoplankton bloom in March 1987. Differences in percent POM between the two locations were most evident in January and February 1987, when percent POM was 10–35% at Avila and 40–70% at Holly (Fig. 3c).

Particulate organic carbon concentration was significantly higher at Avila than at Holly ($t = 4.88$, df = 38, $P<0.001$; Fig. 4). Values at Avila ranged from ~400 µg C/L to ~1400 µg C/L, with values exceeding 1000 µg C/L in late November 1986, and January, April, and June 1987. In contrast, POC concentrations at Holly remained below 500 µg C/L, except during March–April 1987 when values of 650–900 µg C/L were recorded. The peaks in POC concentration at Avila coincided with elevated chlorophyll *a* concentrations in November, April, and June, but not in January. The peaks in POC concentration at Holly coincided with the elevated chlorophyll *a* concentrations in March–April.

The slopes of linear least-square regression lines of POC concentration versus chlorophyll *a* concentration at Avila and Holly were significantly different from 0 ($P<0.05$, ANOVA). There was no significant difference

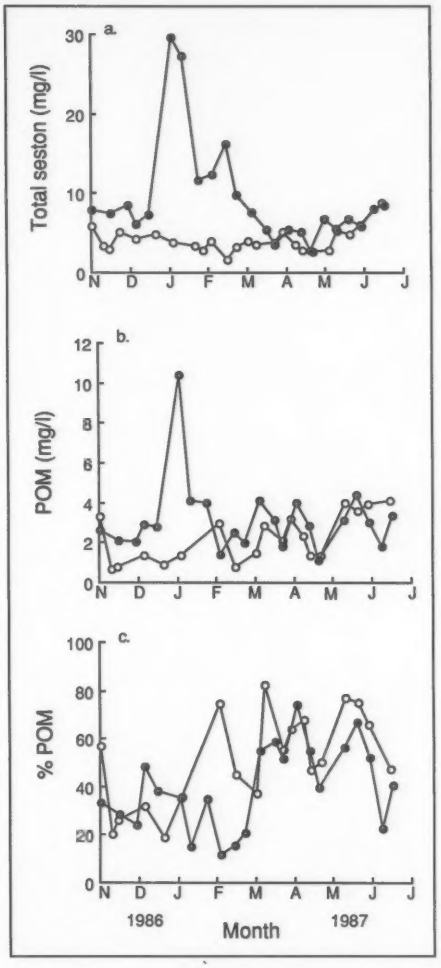

Figure 3
(a) Seston concentrations, (b) particulate organic matter (POM) concentrations, and (c) %POM at Avila Beach (●) and Platform Holly (○).

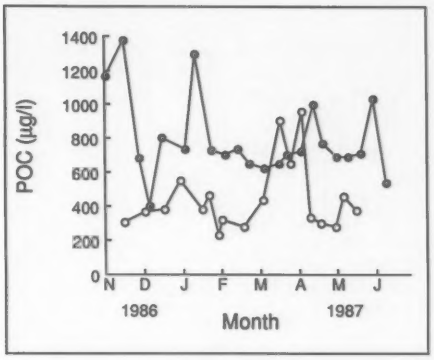

Figure 4
Particulate organic carbon (POC) concentrations at Avila Beach (●) and Platform Holly (○).

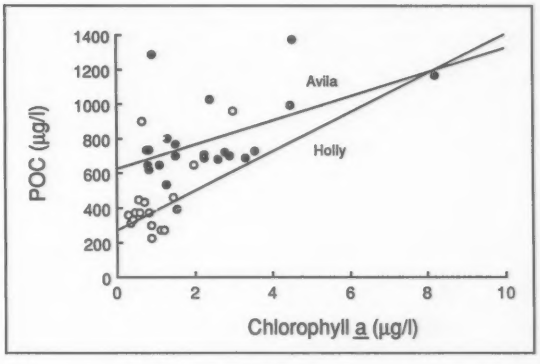

Figure 5
Linear regressions of particulate organic carbon (POC) concentration on chlorophyll *a* concentrations at Avila Beach (●) and Platform Holly (○). Avila: $y = 69.8x + 623$, $r = 0.51$; Holly: $y = 184x + 264$, $r = 0.60$.

in the slopes of these lines ($P>0.1$, ANCOVA; Fig. 5). However, a significant difference in the location of the y-intercepts ($F = 13.46$, df = 1, 34, $P<0.001$, ANCOVA) indicated that a substantially higher concentration of "background" POC existed at Avila (623 µg C/L) than at Holly (264 µg C/L).

Covariance among environmental parameters

We found weak but significant positive correlations between chlorophyll *a* concentration and both water temperature and POC concentration at Avila (Table 2). In contrast, we found a weak negative correlation between chlorophyll *a* concentration and water temperature at Holly. Chlorophyll *a* concentration was positively correlated with both POC and POM concentration at Holly. There was no correlation between chlorophyll *a* concentration and total seston or percent POM, or between POM and POC concentration at either site (Table 2).

Growth rate

Shell growth rates for a mussel of 20 mm shell length over a period of 1 month at Avila and at Holly are given in Figure 6. Growth rate was temporally variable at both locations, with slowest growth rate December–March 1987 (5–7 mm/mo) and most rapid growth

Table 2

Correlation coefficients (r) between factors at inshore (Avila Beach) and offshore (oil platform Holly) locations, calculated from least-squares linear regression analysis. $^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$.

Factors	Avila	Holly
Chlorophyll *a*:Temp	0.48*	−0.36*
Chlorophyll *a*:POC	0.51*	0.60**
Chlorophyll *a*:Seston	−0.27	0.09
Chlorophyll *a*:%POM	0.15	0.40
Chlorophyll *a*:POM	0.11	0.92***
POM:POC	0.02	0.33

Table 3

Results of transplant experiments on *Mytilus edulis* at Avila Beach and oil platform Holly. Mean values ±1 SD.

Treatment	Date	Initial length (mm)	Growth rate (mm/mo)
Avila→Holly	8 Nov. 86	29.9 ± 2.7	8.6 ± 3.1
		30.4 ± 2.9	8.0 ± 2.2
Holly	8 Nov. 86	30.0 ± 2.9	8.1 ± 2.0
		29.2 ± 3.1	7.4 ± 2.0
Holly→Avila	5 Nov. 86	33.3 ± 3.4	7.5 ± 1.9
		35.7 ± 4.2	7.4 ± 1.8
Avila	5 Nov. 86	33.6 ± 2.7	7.6 ± 1.3
		31.6 ± 3.4	7.8 ± 2.3

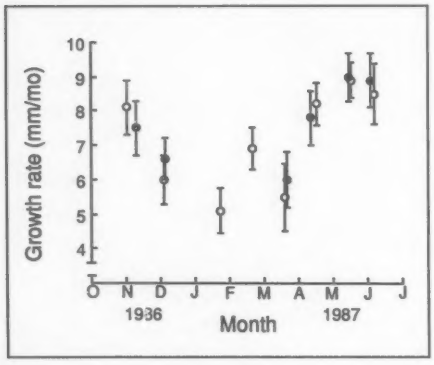

Figure 6

Length-specific growth rate of a 20-mm length *Mytilus edulis* at Avila Beach (●) and Platform Holly (○). Mean values ±95% CI.

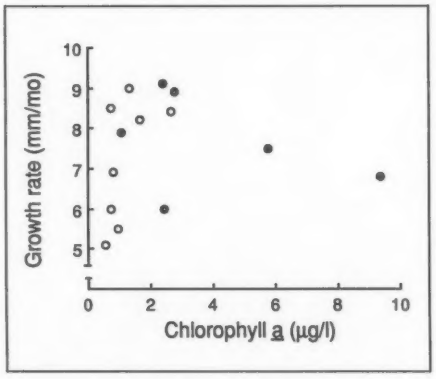

Figure 7

Relationship between *Mytilus edulis* growth rate and chlorophyll *a* concentration with a time lag of 3 weeks at Avila Beach (●) and Platform Holly (○).

October–November 1986 and May–July 1987 (8–9 mm/mo). There was no effect of mussel stock on growth rate ($F = 0.901$, $P>0.1$, 1-way ANOVA; Table 3). Mortality of caged mussels was <5.0%.

Relationship between growth rate and chlorophyll *a* concentration

We calculated correlation coefficients relating the growth rate of *M. edulis* to chlorophyll *a* concentration and water temperature for grouped Avila and Holly data integrated over the 4-week period of mussel exposure and at time lags of 0–4 weeks. There was no correlation between growth rate and chlorophyll *a* concentration ($P>0.05$, $n = 14$). However, growth rate correlated with chlorophyll *a* concentration with a time lag of 3 weeks, if the fall and winter values from Avila (when seston concentrations exceeded 5 mg/L) were excluded ($r = 0.67$, $P<0.05$, $n = 11$; Fig. 7). There was no correlation between growth rate and water temperature ($P>0.05$).

Scope for growth

A summary of our theoretical scope-for-growth calculations, averaged by month, is given in Table 4. Our analysis indicates that, overall, the estimated amount of seston filtered from suspension by mussels was higher at Avila than at Holly (4.00 vs. 1.91 mg/h, $t = 4.03$, df = 46, $P<0.001$). However, mussels at Avila had a significantly higher estimated percent pseudofeces production (48.6% vs. 13.7%, $t = 6.34$, df = 46, $P<0.001$) than mussels at Holly. Thus despite the higher seston concentrations at Avila, the actual amount of estimated POM assimilated by mussels at each locality should have been similar (0.43 mg/h at Holly vs. 0.36 mg/h at Avila, $P>0.01$).

Table 4

Summary of scope-for-growth calculations for a 20-mm shell length (0.05 g) *Mytilus edulis* averaged by month. POM = particulate organic matter.

Month	Clearance rate (L/h)	Seston filtered (mg/h)	Pseudofeces threshold (mg/L)	% pseudofeces	Seston ingested (mg/h)	Absorption efficiency (%)	POM absorbed (mg/h)	VO_2 (mL O_2/h)
Avila Beach								
Nov.	0.45	3.55	3.0	50.62	1.76	42.40	0.23	0.06
Dec.	0.46	3.33	3.0	48.15	1.74	45.38	0.32	0.05
Jan.	0.36	8.03	3.0	74.71	2.26	39.04	0.27	0.04
Feb.	0.42	5.70	3.0	64.59	2.06	27.32	0.31	0.04
Mar.	0.47	3.48	3.0	28.87	2.32	54.94	0.70	0.04
Apr.	0.47	2.22	3.0	23.98	1.72	54.72	0.48	0.04
May	0.46	2.32	3.0	43.21	1.34	54.64	0.43	0.05
June	0.45	3.30	3.0	51.57	1.59	45.88	0.29	0.05
Oil platform Holly								
Nov.	0.48	2.02	3.0	18.58	1.54	42.49	0.24	0.07
Dec.	0.48	1.06	3.0	28.28	1.53	37.29	0.15	0.07
Jan.	0.48	1.58	3.0	0.00	1.58	48.29	0.31	0.05
Feb.	0.48	1.40	3.0	0.00	1.40	55.01	0.48	0.05
Mar.	0.48	1.92	3.0	8.44	1.72	55.90	0.58	0.04
Apr.	0.48	1.42	3.0	0.00	1.42	54.59	0.44	0.05
May	0.48	2.20	3.0	27.12	1.52	60.19	0.65	0.05
June	0.45	3.91	3.0	55.11	1.76	51.65	0.43	0.05

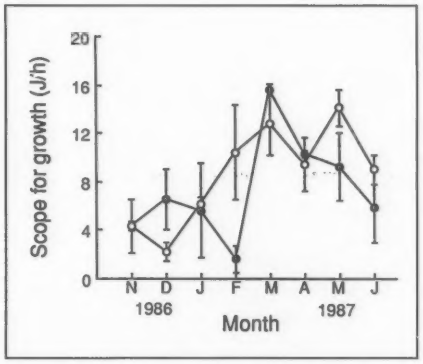

Figure 8

Estimates of monthly scope-for-growth of a 0.05-g dry weight (~20 mm snell length) *Mytilus edulis* at Avila Beach (●) and Platform Holly (○). Mean values ±1 SE.

Table 5

Results of two-way ANOVA evaluating the influence of month and location of estimated scope for growth of *Mytilus edulis*. ***$P<0.001$.

Source	Sum of square	df	Mean square	F ratio
Location	16.09	1	16.09	0.83
Month	557.95	7	79.71	4.11***
Month · Location	190.31	7	27.19	1.40
Error	640.51	33	19.41	

Figure 8 shows the monthly SFG of a 0.05 g dry weight *M. edulis* (~20 mm shell length) at Holly and at Avila, calculated using the seston concentration and percent POM data from these localities and the equations in Table 1. There was a significant effect of month, but not location, on scope for growth (2-way ANOVA, Table 5). An *a posteriori* test for significant differences among months revealed that the low SFG values of November–February differed significantly from the higher SFG values of March–June ($F = 4.11$, df = 1, 33, $P<0.001$).

To evaluate the relationship between shell growth rate and theoretical SFG, we calculated linear correlation coefficients between growth rate (Fig. 6) and scope for growth for the combined Avila and Holly data at time lags of 0–4 weeks. Growth was not correlated with SFG at a time lag of 0 weeks ($r = 0.56$, $P>0.05$). However, growth rate correlated with SFG at time lags of 1–4 weeks with strongest correlations at time lags of 2 and 3 weeks ($r = 0.70$ and 0.75, $P<0.05$, $n = 10$; Fig. 9).

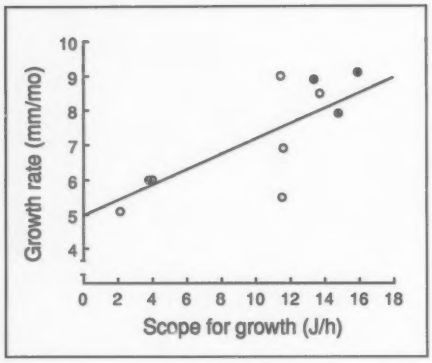

Figure 9
Linear regression of *Mytilus edulis* shell growth rate on scope for growth for combined data from Avila Beach (●) and Platform Holly (○) with a time lag of 3 weeks. $y = 0.22x + 4.96$, $r = 0.75$.

Discussion

Spatial variation in phytoplankton biomass may affect the growth and nutritional condition of filter-feeding species along the California coast (larval fish *Engraulis mordax*, Lasker and Smith 1977, O'Connell 1980; copepod *Calanus pacificus*, Willason et al. 1986; anomuran crab *Emerita analoga*, Dugan and Wenner 1985). We found that mussel growth increased with chlorophyll *a* concentration, except during the fall and winter months at Avila. The low growth rates at Avila during fall and winter, despite chlorophyll *a* concentrations exceeding 4 μg/L, may reflect a leveling-off or decline in particle ingestion rates associated with high seston concentrations (Foster-Smith 1975, Widdows et al. 1979).

Temporal patterns of growth were similar for mussels at Avila and Holly (Fig. 6). These data suggested that ingestion rate was not appreciably higher for mussels at Avila, despite the higher POC concentrations there (generally >600 μg/L). In addition, both the high background POC concentration (623 μg/L, Fig. 5) and the lack of correlation between chlorophyll *a* and POM concentrations at Avila indicated the presence of a high concentration of nonphytoplankton particulates (e.g., bacteria, microzooplankton, detritus) which may not support rapid mussel growth. *Mytilus edulis* has shown poor growth when supplied only with nonphytoplankton food sources in laboratory experiments (Winter 1974, Williams 1981).

The lack of a correlation between growth rate and water temperature for grouped data from both locations is consistent with the view that water temperature is not an important factor influencing mussel growth in California waters (Page and Hubbard 1987).

The lack of a stock or genotypic effect on mussel growth rate in our transplant experiments was not surprising, as the distance between the study sites was only about 120 km. *Mytilus edulis* has a planktonic larval stage of about 3 weeks, and typical current velocities of 0.5 km/hour (Chambers Group 1986) would permit larvae to drift as much as 250 km. *Mytilus edulis* also has the potential to delay metamorphosis and to exist as a pediveliger in the plankton for several days (Bayne 1964), facilitating genetic exchange between spatially separated populations. The transplant experiments also indicated that postsettlement selection (Koehn and Hilbish 1987), which might result in differences in growth rate between locations, was not an important factor in this study.

Our field growth-rate data generally conform to predictions from the theoretical SFG analysis. This analysis suggested that mussels at Avila and Holly absorbed similar amounts of POM and had similar SFG because seston concentrations were high at Avila (>4 mg/L) and mussels at this location had a higher rate of pseudofeces production and lower absorption efficiency than mussels at Holly. Shell growth rate correlated with theoretical SFG after incorporation of a time lag. SFG is a measure of the energy instantaneously available for the growth of soft tissue and shell. In small mussels, shell growth rate is correlated with soft tissue growth (Nielsen 1985). The time lag likely reflects the time required for metabolic conversion of absorbed energy and nutrients into the shell.

The relationships between potential food availability and mussel growth at Avila and Holly agree with general predictions developed primarily from physiological studies of *M. edulis* in British estuarine environments where the energy available for growth was regulated by the food quality, reflected by the percent POM, rather than by quantity of the seston when seston concentrations exceeded 4–5 mg/L (Bayne and Widdows 1978, Widdows et al. 1979). The growth rate of mussels in California coastal waters, with seston concentrations comparable to those at Avila, is thus likely limited by the quality rather than the quantity of the seston.

Acknowledgments

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Recent Fluctuations in the Abundance of Baleen Whales in the Southern Gulf of Maine in Relation to Changes in Selected Prey

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Abstract.–Significant changes in the biomass of sandlance *Ammodytes* spp. and in the abundance of the copepod *Calanus finmarchicus* in the southern Gulf of Maine co-occurred with a shift in the occurrence and abundance of four species of baleen whales in the region. During the years 1982–88 the abundance of sandlance was negatively correlated to the abundance of *C. finmarchicus* ($r_s = -0.883$, $P<0.05$). Peak years of abundance for *C. finmarchicus* during 1982–88 in the study area were the lowest years of abundance for sandlance. The abundance of *C. finmarchicus* and sandlance was at a regional maximum during 1986 and 1988, respectively.

The abundance of humpback and fin whales were marginally correlated to each other ($r_s = 0.3338$, $P< 0.08$). The abundance of humpbacks was negatively correlated with right whales ($r_s = -0.7753$, $P<0.001$) and sei whales ($r_s = -0.5507$, $P<0.01$). The patterns of occurrence for right and sei whales were significantly related to each other ($r_s = 0.6842$, $P< 0.001$). Right and sei whales were common in the region only during 1986, when copepod abundance reached a regional maximum and sandlance abundance a regional minimum. These patterns of whale occurrence reflect known prey preferences, and are therefore expected between the pisciverous humpback and fin whales and the highly planktiverous right and sei whales.

We hypothesize that the spatial distribution and abundance of baleen whales in the Gulf of Maine can be characterized as a series of ecological responses to human-induced changes in the abundance of planktiverous finfish.

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Fishery Bulletin, U.S. 88:687–696.

During the mid-1970s, a dramatic increase in the abundance of sandlance *Ammodytes* spp.* precipitated a significant change in the abundance and composition of the ichthyofauna in the shelf waters of the northeastern United States (Smith et al. 1978, 1980; Morse 1982). The population explosion of sandlance coincided with a 50% reduction in total finfish biomass in the same region between 1968 and 1975 (Clark and Brown 1977). This decrease was primarily due to the commercial depletion of stocks of herring *Clupea harengus* and mackerel *Scomber scombrus* (Anthony and Waring 1980, Grosslein et al. 1980). A concurrent increase in sandlance abundance following the depletion of North Sea herring and mackerel stocks led Sherman et al. (1981) to suggest that sandlance had taken over ecological niches previously occupied by these species in many areas of the Northwest Atlantic.

Since the mid-1970s sandlance have become increasingly important in the Gulf of Maine as prey for commercial fish (Bowman et al. 1984), seabirds (Powers and Backus 1987), pinnipeds (Payne and Selzer 1989), and baleen whales (Overholtz and Nicolas 1979, Hain et al. 1982, Payne et al. 1986). Sandlance were the only confirmed prey of the humpback whale *Megaptera novaeangliae* between 1975 and 1979 (Hain et al. 1982, Mayo 1982) and the only prey significantly correlated with the distribution of humpbacks in the Gulf of Maine between 1978 and 1982 (Payne et al. 1986). Also, fin whales *Balaenoptera physalus*, sympatric with humpbacks in this region, have frequently been observed exploiting sandlance (Overholtz and Nicolas 1979).

Two other species of large baleen whales, the northern right whale *Eubalaena glacialis* and the sei whale *Balaenoptera borealis*, also occur in

*Two species of this genus, *A. americanus* and *A. dubius*, occur in the shelf waters of the northeastern United States (Richards et al. 1963, Reay 1970, Richards and Kendall 1973, Meyer et al. 1979, Richards 1982).

the Gulf of Maine (CeTAP 1982, Watkins and Schevill 1982, Kraus 1985, Schevill et al. 1986, Weinrich et al. 1986, Hamilton and Mayo 1990). Both of these species have been characterized principally as "skim feeders" (Nemoto 1959, Kawamura 1974, Nemoto and Kawamura 1977) which subsist primarily on dense swarms of calanoid copepods, notably *Calanus finmarchicus* in the North Atlantic (Mitchell 1975a, 1975b; Jonsgard and Darling 1977; Mitchell and Chapman 1977; Winn et al. 1986; Wishner et al. 1988; Mayo and Marx 1990), in preference to schooling fish (Watkins and Schevill 1979).

This similarity in prey preference led Mitchell (1975a) to hypothesize that competition between these two whale species might have adversely affected the recovery of the right whale in the western North Atlantic. However, sandlance are also known to play an important trophic role as a major predator of copepods, especially *C. finmarchicus* (Monteleone and Peterson 1986, Meyer et al. 1979). Given their abundance and prey selectivity towards copepods, Kenney et al. (1986) proposed that sandlance represented a more significant competitor to right whales for copepodite prey than sei whales (as suggested by Mitchell 1975a).

The existence of some degree of intra- and interspecific competition between right/sei whales and sandlance (ecologically similar species) for a common prey is generally accepted, but is difficult to demonstrate. An overlap in preferred prey is at best a qualitative phenomenon, and offers only "soft corroboration" (from Strong et al. 1984) as evidence for competition between these species. Another approach (used by Smith 1968, 1970; Eck and Wells 1987), which we have adopted for the purpose of this study, is to look for a demonstrable shift in the ecological balance between competing species, or the complete replacement of one competing species by another. In this paper we examine the ecological relationships between sandlance and two of its major predators, the humpback and fin whale; between sandlance and its major prey, the copepod *Calanus finmarchicus*; and between sandlance and two potential competitors for *C. finmarchicus* in this region, the right and sei whale.

Methods

Study area

In this paper we have focused on Stellwagen Bank (Fig. 1), a glacial deposit of sand and gravel in the southwest Gulf of Maine that is associated with high levels of biological productivity and a rapidly developing commercial whalewatching industry. The margins of the bank are defined by the 40-m isobath with depths as low as 18 m. Since the early 1980s whalewatching vessels have provided intensive survey coverage of cetaceans in the area from June through September of each year.

Collection and treatment of data

Fisheries data Data on the abundance of sandlance used here were collected on Stellwagen Bank and immediately adjacent waters by National Marine Fisheries Service, Northeast Fisheries Center (NMFS/NEFC) biologists and technicians during standardized NMFS/NEFC spring bottom-trawl surveys. The NMFS/NEFC survey area has been spatially stratified into approximate ecological units based principally on depth (see Grosslein 1969). Stellwagen Bank is a principal bathymetric feature in the Gulf of Maine–NMFS/NEFC stratum #26. The number of sandlance caught per tow in stratum #26 (for each spring survey) was transformed into logarithmic values, and the mean number of sandlance (transformed data) was considered representative of Stellwagen Bank and used in all further analyses, a procedure which follows that described in Payne et al. (1986).

The *Calanus finmarchicus* data were also collected by NMFS/NEFC personnel. A transect across the Gulf of Maine has been sampled with the Hardy Continuous Plankton Recorder (CPR) since 1961 (Jossi and Smith 1990). Since the early 1980s a desired sampling frequency of one transect per month has been generally achieved. Data used in this study came from the 10-nautical-mile section of the transect centered on Stellwagen Bank. Water passing through the CPR is filtered with bolting silk having mean aperture dimensions of 225 × 234 μ. All large zooplankton ($\geq$2 mm) in the sample are identified and enumerated. Counts of smaller ($\leq$2 mm) zooplankton are made from an aliquot ($\sim$1/45) of the sample. Counts were converted to number of organisms per 100 m^3, and then transformed to log base 10 for subsequent calculations. Further details of this procedure are given in Colebrook (1975) and in Jossi and Smith (1990). All reference to copepod data and abundance used in this study exclusively concern *C. finmarchicus*.

The abundance of sandlance (expressed as the mean of the log-transformed number of sandlance per tow/year) and of the copepod *C. finmarchicus* (log-transformed number of individuals/100 m^3/year) were compared by first ranking the data by year, 1982–88 (N = 7), then calculating Spearman's coefficient of rank correlation (r_s) (Zar 1984). The data are therefore compared on an ordinal, rather than on an absolute, scale; this is because of the magnitude of the difference in the scale of the data that were brought together for this study.

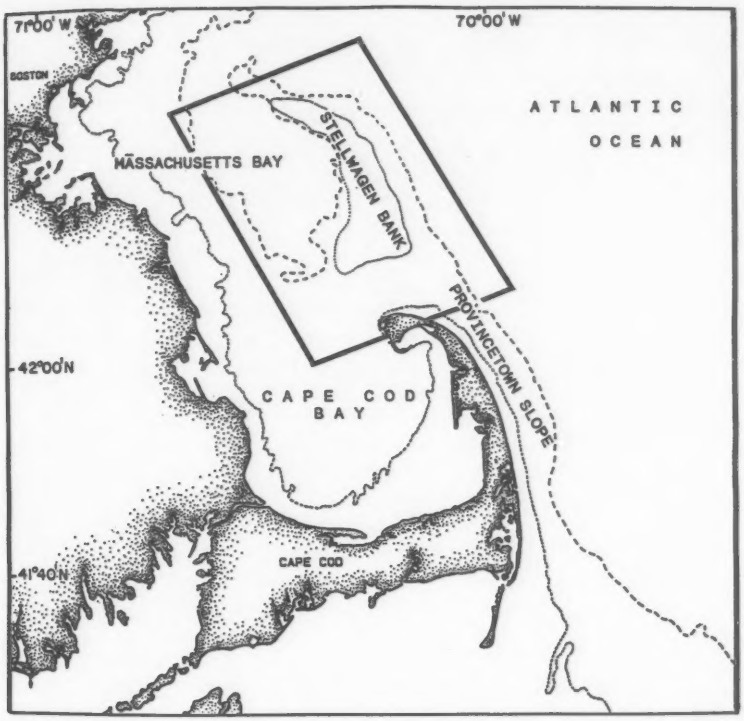

Figure 1
Baleen whale study area in southern Gulf of Maine (outlined) and geographical regions referred to throughout the text.

Whale sighting data Data for this study on the occurrence and distribution of humpback, fin, right, and sei whales were collected by naturalists working aboard commercial whalewatching vessels during the study period 1982–88. Data recorded from these vessels for all cetacean sightings include species, group size, time, location (using LORAN-C), behavior, and the photographically confirmed identity of individual animals. Vessels ran 4-hour cruises to the Stellwagen Bank and Massachusetts Bay areas from two ports: Provincetown and Plymouth, Massachusetts. The cruise track of the whalewatching vessels was decided by the captain based upon the greatest number of whale sightings recorded on the previous trip or day; consequently, sampling was neither random nor systematic. Nonetheless, the intensity of the coverage resulted in extremely comprehensive surveys of the region during most of the study period. The information collected aboard these vessels in this region represents one of the most detailed databases available anywhere on a multispecies group of whales.

Data used in this study were taken from the first cruise of each day from each of the two ports and considered a reliable index of relative abundance of whales in the area. The total number of whales observed during each morning whalewatching trip from each port was summed by species and month, June–September (the period when coverage from whalewatching vessels was effectively continuous). These totals were then divided by the number of trips each month (each trip was considered a unit of effort), resulting in an index of whale abundance, expressed as number of whales/effort/month for each species between 1982 and 1988. While there are undoubtedly biases associated with the collection of these data, the intensity of coverage is such that this index can be used to accurately monitor relative changes in the local abundance and distribution of whales.

Using these sighting data, the temporal co-occurrence between the four whale species within the study area was tested by ranking the mean number of whales/effort/month (by species), then calculating Spearman's coefficient of rank correlation (r_s) (Zar 1984) between species for all paired data, 1982–88 ($N = 28$ for each possible pairing).

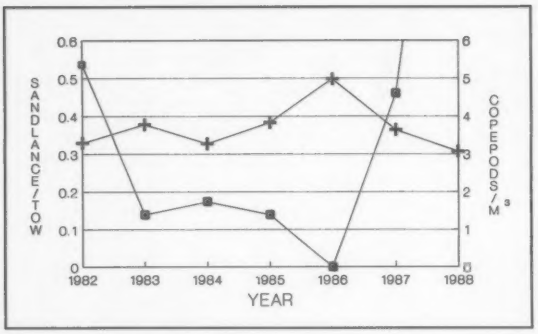

Figure 2

Stratified mean number of sandlance (■) per tow (log transformation) on left, and the number of copepods *Calanus finmarchicus* (+) per m^3 (log transformation) on right. Note: the scale for sandlance is different from that of copepods.

Results

Changes in abundance of sandlance and copepods

The mean number of sandlance per tow (log transformation) collected during spring bottom-trawl surveys ranged between years (Fig. 2) from a minimum 0.000 (in 1986) to a maximum 4.066 per tow (in 1988). Two trends were apparent. The data show a decline in catches from 1982 to the zero value of 1986. Catches increased in 1987, peaking in 1988 to 4.066 sandlance per tow (log value). The number of sandlance caught in 1988 was a regional abundance maximum for spring surveys, 1968–88 (from information presented in Nelson and Ross 1989).

The log-transformed values of *C. finmarchicus*/m^3 of water collected in the CPR ranged from 3.270 (in 1984) to 4.988 (in 1986), and generally increased on Stellwagen Bank between 1982 and 1986 (Fig. 2). The increase was most apparent between 1984 and 1986. The number of *C. finmarchicus* collected in 1986 was one order of magnitude greater than that collected during any other year of the study. Following 1986 the number of *C. finmarchicus* declined rapidly to 3.640 (log value) in 1987, then to 3.070 (log value) in 1988 (Fig. 2).

The abundance of sandlance on Stellwagen Bank was inversely related to the abundance of *C. finmarchicus* ($r_s = -0.883$, $P<0.05$, $N=7$). The three years when the spring tow values for sandlance were the lowest (1983, 1985, and 1986) were the three peak years for *C. finmarchicus* (Fig. 2). Conversely, the number of *C. finmarchicus* recorded on Stellwagen Bank during 1988 was one of the lowest throughout the study period. This is the year when the sandlance reached its maximum peak of abundance.

Changes in whale abundance

Humpback and fin whales showed a similar trend in abundance ($r_s = 0.3338$, $P<0.074$, Table 2), although the variation in the observed number of humpbacks between years was much more pronounced than for fin whales. The number of humpbacks/year increased from 3.59 whales/effort in 1982 to 9.00 whales/effort in 1985 (Table 1, Fig. 3). During 1986 humpback abundance declined to the minimum value recorded during the study period of 0.23 whales/effort. A small increase in 1987 was followed by a much larger increase in 1988 to 6.98 whales/effort (Fig. 3).

Less dramatic fluctuations between years were evident in the number of fin whales from 1982 to 1988. The abundance of fin whales declined from the maximum value of 3.71 whales/effort in 1984 to the low values of 1.9 and 1.4 whales/effort recorded in 1986 and 1987, respectively (Fig. 3). Although the numbers of fin whales/effort were lower in 1986–87 than in previous years, they did not change by more than an order of magnitude, as did other whale species. The number of fin whales increased to 3.61 whales/effort in 1988.

The strongest positive correlation occurred between right and sei whales ($r_s = 0.6842$, $P<0.0001$, Table 2). The right whale is a rare but regularly occurring species whose temporal occurrence in the study area has been generally restricted to the months of late-winter through early-spring (Winn et al. 1986, Brown and Winn 1989, Hamilton and Mayo 1990). This pattern was generally repeated in all years of the study period except 1986. Excluding 1986, there were only 12 right whale sightings from 1982 to 1988, and during most years there were no sightings (Table 1). However, in 1986, 174 right whale sightings (0.95 whales/effort) were recorded, and right whales were observed virtually every day throughout the summer (Hamilton and Mayo 1990).

Sightings of sei whales on Stellwagen Bank, and in Cape Cod Bay, are very rare in any season (CeTAP 1982, Mayo et al. 1988). We did not observe sei whales in the study area between 1982 and 1985 (Table 1). However, their numbers increased significantly in 1986 (when they were commonly observed) to 0.26 whales/effort (Table 1, Fig. 3). The occurrence of sei whales in 1986 was followed by an equally dramatic decline during 1987 (2 sightings, 0.01 sei whales/effort) and 1988 (no sightings). Between 1982 and 1988, the sei whale and right whale were abundant only during 1986 (Fig. 3), when the abundance of *C. finmarchicus* also reached a recorded regional maximum (Wishner et al. 1988).

Table 1

Total number of whales counted, number of surveys (effort), and number of whales (by species) per survey in southern Gulf of Maine (in parentheses) for each month and year of the study, 1982–88.

Year	Month	No. of surveys	No. of whales (per survey)			
			Humpback	Fin	Right	Sei
1982	June	27	90(3.33)	45(1.67)	0.00	0.00
	July	31	228(7.35)	33(1.06)	0.00	0.00
	Aug.	31	54(1.74)	227(7.32)	0.00	0.00
	Sept.	27	45(1.67)	63(2.33)	4(0.15)	0.00
	Total	116	417(3.59)	368(3.17)	4(0.03)	0.00
1983	June	46	229(4.98)	60(1.30)	0.00	0.00
	July	43	266(6.19)	192(4.47)	0.00	0.00
	Aug.	36	169(4.69)	172(4.78)	0.00	0.00
	Sept.	28	96(3.43)	37(1.32)	0.00	0.00
	Total	153	760(4.97)	461(3.01)	0.00	0.00
1984	June	43	317(7.37)	26(0.60)	0.00	0.00
	July	45	382(8.49)	224(4.98)	0.00	0.00
	Aug.	47	261(5.55)	232(4.94)	0.00	0.00
	Sept.	33	133(4.03)	141(4.27)	0.00	0.00
	Total	168	1093(6.51)	623(3.71)	0.00	0.00
1985	June	40	411(10.30)	143(3.58)	0.00	0.00
	July	53	400(7.55)	122(2.30)	0.00	0.00
	Aug.	46	654(14.21)	154(3.35)	0.00	0.00
	Sept.	31	63(2.03)	24(0.78)	0.00	0.00
	Total	170	1528(8.99)	443(2.61)	0.00	0.00
1986	June	44	16(0.36)	62(1.41)	2(0.05)	0.00
	July	54	20(0.37)	136(2.52)	6(0.11)	2(0.04)
	Aug.	51	4(0.08)	93(1.82)	44(0.86)	19(0.37)
	Sept.	34	2(0.05)	102(3.00)	122(3.58)	26(0.76)
	Total	183	42(0.23)	344(1.88)	174(0.95)	47(0.26)
1987	June	55	30(0.55)	56(1.02)	2(0.04)	0.00
	July	61	36(0.59)	48(0.79)	1(0.02)	2(0.03)
	Aug.	55	76(1.38)	150(2.73)	0.00	0.00
	Sept.	47	12(0.25)	52(1.10)	5(0.11)	0.00
	Total	218	154(0.71)	306(1.40)	8(0.04)	2(0.01)
1988	June	55	199(3.62)	253(4.60)	0.00	0.00
	July	62	535(8.63)	263(4.24)	0.00	0.00
	Aug.	62	455(7.34)	160(2.58)	0.00	0.00
	Sept.	52	424(8.15)	159(3.06)	0.00	0.00
	Total	231	1613(6.98)	835(3.61)	0.00	0.00

Table 2

Spearman Rank Correlation Coefficients (r_s) (upper number) and statistical level of significant difference (P) (lower number) between the abundance (whales/effort) of four baleen whale species on Stellwagen Bank, 1982–88. N = 28 for all paired tests.

	Humpback	Fin	Right	Sei
Humpback	1.0000	0.3338	−0.7753	−0.5507
	0.0000	0.0740	0.0001	0.0019
Fin		1.0000	−0.3250	−0.1461
		0.0000	0.0643	0.4248
Right			1.0000	0.6842
			0.0000	0.0001
Sei				1.0000
				0.0000

Several significant negative relationships also occurred between whale species (Table 2), most noticeably between humpbacks and right whales ($r_s = -0.7753$, $P<0.0001$), humpbacks and sei whales ($r_s = -0.5507$, $P<0.0019$), and fin whales and right whales ($r_s = -0.3250$, $P<0.0643$). This supports an intuitive interpretation of the data shown in Figure 3, notably the obvious phenomenon of low humpback and fin whale abundance in 1986, the only year right and sei whales were observed in significant numbers.

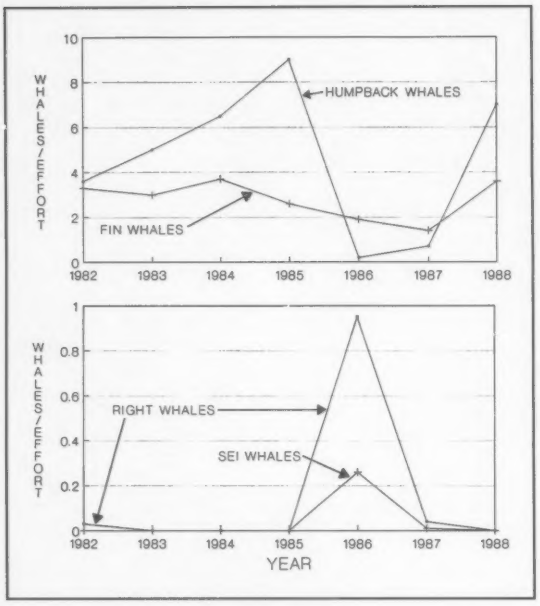

Figure 3
Average number of baleen whales per unit effort for each year of the study by species. Note: the scale for humpback and fin whales (upper) is different from that of right and sei whales (lower).

Discussion

The data presented here strongly suggest that major changes which occurred in the abundance and distribution of humpback, fin, right, and sei whales in the Stellwagen Bank area, 1982–88, were not independent of each other. During 1986 a dramatic decline in the abundance of humpback and fin whales also co-occurred with the unusual occurrence of right and sei whales during the summer of the same year. During 1987 and 1988 the abundance of baleen whales returned to a pattern similar to that observed in years prior to 1986 (right and sei whales absent, humpback and fin whales abundant). Concurrent with changes in whale abundance, an increase in copepod abundance on Stellwagen Bank in 1986 correlated with a significant decline in local sandlance abundance.

These correlations likely reflect both the similarities and dissimilarities in prey preferences of individual whale species, and the predator-prey relationship between sandlance and copepods. Given the documented preference of both right and sei whales for copepods (Nemoto 1959, Mitchell 1975a, Nemoto and Kawamura 1977, Watkins and Schevill 1979), a strong positive correlation between the two species should be expected. A similar correspondence exists between humpback and fin whales, both of which show an apparent preference for schooling fish in this region (Watkins and Schevill 1979, Mayo et al. 1988). Conversely, the strong negative correlations reported here would be expected between the planktiverous right and sei whales and the pisciverous humpback and fin whales.

Competition between whale species

These results, in support of previous studies (Kenney et al. 1981, Payne et al. 1986), suggest that the recent distribution of humpback whales in the Gulf of Maine has been dependent on the spatial distribution of sandlance in that region. These results follow a trend which began in the mid-1970s and, when taken with the results of previous studies (Overholtz and Nicolas 1979, CeTAP 1982, Hain et al. 1982, Mayo 1982, Mayo et al. 1988), indicate that sandlance has been the most important prey item of humpback whales in the Gulf of Maine since at least 1976.

It is also of interest that, while fin whales also closely followed the abundance patterns of sandlance, the overall changes in fin whale abundance fluctuated much less than those shown for the humpback whale. Although both whale species prey on a variety of taxa (Jonsgaard 1966) and have been characterized as generalists in their dietary preferences (Mitchell 1975a), behavioral differences between the two species may result in the ability of fin whales to exploit prey other than sandlance in the study area.

Watkins and Schevill (1979) noted clear differences between the feeding behavior of humpback and fin whales when exploiting the same prey (schooling fish); fin whales lunge horizontally and humpbacks vertically. Humpbacks are also known to produce "bubble clouds or nets" to potentially concentrate prey (Jurasz and Jurasz 1979, Hain et al. 1982, Hays et al. 1985), a feeding method not observed for fin whales. It has also been suggested that the streamlined form and greater speed of fin whales allow them to exploit more widely separated patches of prey than humpbacks (Brodie 1975, Whitehead and Carlson 1988). Thus fin whales may be more independent of local fluctuations in prey availability, explaining why they were located in the study area in 1986, after humpbacks had abandoned it.

Evidence clearly exists to support the belief that competition exists between right and sei whales (Mitchell 1975a, Kawamura 1978). However, Kenney et al. (1986) suggested that competition between right and sei whales in the shelf waters of the northeastern United States is unlikely given their present allopatric distributions (excluding 1986). Perhaps the more important ecological question concerns the reason for the present apparent allopatry. As detailed below, we

believe that this recent distributional change has resulted from differing degrees of interspecific competition between each of the two whale species and sandlance, moreso than from any competition between the whales themselves.

Competition between sandlance and planktiverous whale species

Historically, and in recent times, right whales have been recorded in the Stellwagen Bank region in late winter and early spring (Allen 1908, Allen 1916, Watkins and Schevill 1982, Schevill et al. 1986, Hamilton and Mayo 1990). The species has been virtually absent from the area in summer, when the population's distribution is centered in the Bay of Fundy and on the Scotian Shelf (Kraus et al. 1982, 1986; Mitchell et al. 1986; Winn et al. 1986; Stone et al. 1988; Murison and Gaskin 1989). Therefore, the prolonged residency by a group of right whales in the Stellwagen region throughout summer 1986 may represent the most significant departure from their usual seasonal pattern of occurrence recorded this century.

Is the annual movement of right whales out of the southern Gulf of Maine and into the Bay of Fundy and Scotian shelf areas in early summer related to increased activity and competition from planktiverous fish for calanoid copepods? The question of why right whales generally undertake this northward migration has yet to be resolved. The occurrence of right whales in the Stellwagen Bank area in the summer of 1986 implies that, if certain conditions are met, the normal northward movement is not inevitable for at least part of the population. The occurrence of planktiverous fish (either sandlance, herring or mackerel)—and consequently of increased competition through predation on, or disruption of, copepod patches in spring—may be a major factor in directing the seasonal movement of right whales out of the area to seek more acceptable patches elsewhere in the Gulf of Maine.

Not only are the size and density of copepod patches important to the feeding energetics of right whales, but also the relative proportions of adult copepods within each patch (Wishner et al. 1988). Wishner et al. (1988) described a copepod surface patch (with associated skim-feeding right whales) which contained a regional maximum of copepodite IVs and Vs, the older, energetically richest, developmental stages of copepods (Comita et al. 1966). Although the feeding ecology of right whales is likely more complex than previously thought (Mayo and Marx 1990), these dense aggregations of older, caloric-rich copepods seem to be the required characteristics for energetically successful foraging by right whales (Kenney et al. 1986, Wishner et al. 1988).

The principal diet of sandlance >21 mm is also the larger, older developmental stages of *C. finmarchicus* (Norcross et al. 1961, Scott 1973, Monteleone and Peterson 1986). If the superabundant sandlance are selecting the caloric-rich stages of the copepod population, then there may be insufficient prey available in the remaining developmental stages (independent of abundance) to provide right whales with the required energy densities (as described by Kenney et al. 1986) to meet the metabolic and reproductive demands of the right whale population. Therefore, during those years when sandlance (or ecologically similar planktiverous fish species) are abundant, intraspecific competition may be so intense that right whales may only be achieving basal metabolic needs in the southern Gulf of Maine, precipitating the northward movement of right whales immediately following the period of increased sandlance abundance and activity.

The occurrence of consistent numbers of sei whales in 1986 followed many years in which the species had not been recorded from the study area during any season (Mayo et al. 1988). Jonsgaard and Darling (1977) describe "invasion years" where unusually large numbers of sei whales occur in an area. These years are generally followed by an equally sharp decrease in the number of whales in the same area. Albeit simple, an "invasion year" in response to increased prey abundance accurately describes the occurrence of sei whales on Stellwagen Bank during 1986.

While sei whales seem to prefer planktonic prey (Watkins and Schevill 1979), they have the ability to forage on fish (Nemoto 1959, Nemoto and Kawamura 1977). Despite this, available distributional evidence suggests that sei whales have not exploited the abundant sandlance in the Gulf of Maine to a significant extent. Scant data suggest that sei whales in this region instead subsist primarily on euphausiids and copepods which occur in the waters south of Georges Bank (Kenney and Winn 1987). By remaining on the shelf edge and exploiting a wider range of planktonic (and possibly fish) prey, they may be able to minimize the effect of competition from sandlance for copepods, separating them from the more stenophagic right whales.

Since the early 1950s sandlance populations have fluctuated on remarkably few occasions. Monteleone et al. (1987) described relatively high sandlance densities during 1965–66 (following the depletion of herring and mackerel stocks) and 1978–79 (following the larval sandlance explosion in 1975), and exceptionally low densities of sandlance in 1971–74. Meyer et al. (1979) also reported that adult sandlance were not reported on Stellwagen Bank between 1967–76 and that the mean sandlance catch/10 m^2 in spring 1977 was nine times greater than in spring 1974. Therefore, the two recorded time intervals when sei whales and

right whales were most abundant in the study area (April 1970, reported by Watkins and Schevill 1982; and during 1986) were during periods of documented low adult sandlance densities and observed copepod maxima. The March 1975 observations by Watkins and Schevill (1979) of a sei and right whales feeding together in Cape Cod Bay were also made in the interval between the reduction of planktiverous herring and mackerel stocks and the subsequent population explosion of adult sandlance. These observations further support the theory that planktiverous fish abundance has negatively impacted the occurrence of planktiverous whale species in the region.

In this paper, we have examined species interactions between sandlance (as prey and competitor), *C. finmarchicus* (as prey), and the abundance of four species of baleen whales in the southern Gulf of Maine. The interpretation of these interactions, although largely inductive, provide useful management insights into the relationships between planktiverous finfish and the cetacean community. This interpretation also presents an interesting multispecies-management dilemma regarding finfish and cetacean populations in this region, as well as potential conflicts between single-species recovery plans and two ecologically different groups of endangered whales, pisciverous and planktiverous.

The present abundance of sandlance in the Gulf of Maine followed a long-term depletion of other planktiverous fish species through overfishing (Grosslein et al. 1980). Although it is impossible to reconstruct the extent of competition between finfish (herring and mackerel stocks) and planktiverous whales prior to the mid-1960s, the similarities in prey preference and trophic relationships between mackerel, herring and sandlance (Bowman et al. 1984) certainly suggest that competition between herring-mackerel stocks and planktiverous whales could have existed. We hypothesize that the abundance and distribution of planktiverous fishes have played a significant, perhaps critical, role in structuring (as prey and competitor) baleen whale populations in the Gulf of Maine.

The present, concentrated distribution of humpbacks in the Gulf of Maine is directly related to the distribution and increased abundance of sandlance in that region. Alternatively, the recovery of the stenophagic right whale (historically and at present) may indeed be inhibited in large regions of the northwest Atlantic by competition for its prey by herring, mackerel, and sandlance. Despite decades of protection Schevill et al. (1986) suggested that the [abundance of the] right whale population [now] which passes Cape Cod is "at worst slightly smaller than it was in the 17th century". The abundance and distribution (and continued recovery) of right whales, in contrast to humpback and fin whales, may be contingent upon anomalous disruptions in the occurrence of abundant, ecologically equivalent finfish stocks, which at present are largely human-induced.

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Abstract.– Coastal cutthroat trout and steelhead, which are sympatric over much of their range along the Pacific coast of North America, have different behaviors in both freshwater and the ocean. Juveniles of both species were caught in purse seines off the Oregon and Washington coasts during the early summer, sometimes over 46 km offshore. However, both species were absent from catches in September. Cutthroat apparently returned to freshwater, whereas steelhead migrated far offshore during late summer. Ocean growth rates of smolts of both trouts were similar, about 1 mm per day; but since cutthroat spend little time in the ocean, they are small at maturity. This is possibly an adaptation related to spawning short distances from the ocean or in small tributaries upstream of the spawning and rearing habitats of other anadromous salmonids. Cutthroat trout fed primarily on fishes, but steelhead had a more varied diet in coastal waters, consuming fishes but also euphausiids and other crustaceans.

Distribution and Biology of Juvenile Cutthroat Trout *Oncorhynchus clarki clarki* and Steelhead *O. mykiss* in Coastal Waters off Oregon and Washington

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Two species of anadromous trout are native to the Pacific coast drainages of North America: *Oncorhynchus c. clarki* (formerly *Salmo c. clarki*), the coastal cutthroat trout, and *O. mykiss* (formerly *Salmo gairdneri* and *S. mykiss*), the steelhead and Kamchatkan trout (Smith and Stearley 1989). The coastal cutthroat trout ranges from northern California to southeastern Alaska. The native range of the steelhead trout was from the Alaska Peninsula to Baja but now is found only as far south as central California (Carl et al. 1959, MacCrimmon 1971, Scott and Crossman 1973).

Because these two trout species are sympatric over much of their range (Scott and Crossman 1973, Behnke 1979) behavioral and ecological differences are of special interest. Coastal cutthroat select small tributaries for spawning, rarely over 160 km inland, whereas steelhead prefer larger streams and sometimes migrate long distances from the ocean. Coastal cutthroat usually spawn slightly earlier in the year (January–March) than steelhead (February–April) (Needham and Gard 1959, Withler 1966, Hartman and Gill 1968, Scott and Crossman 1973, Johnston 1982). These differences in location and time of spawning apparently help maintain reproductive isolation between these species (Needham and Gard 1959, Trotter 1989).

Anadromous wild stocks of both species of trout usually spend 2–4 years in freshwater before smoltification and downstream migration to the ocean, while hatchery stocks commonly migrate to the sea after one year in freshwater. Downstream migrations of smolts of both species usually peak in April or May (Chapman 1958, Lowry 1965, Withler 1966, Armstrong 1971, Giger 1972, Sutherland 1973, Okazaki 1984, Dawley et al. 1985, Loch and Miller 1988) or in late May or early June in Alaska (Armstrong 1971).

Our knowledge of the marine life history and ecology of steelhead and cutthroat trout is meager. In this

paper we describe the distribution and movements, age and size distribution, sex ratios, and food habits of juveniles of these species in coastal waters off Oregon and Washington as determined by purse seine catches, discuss the differences between these species, and speculate on their adaptive significance.

Methods

Cutthroat trout and steelhead were captured in purse seines in the northeastern Pacific Ocean during May–September, 1980–85. Data from 1981–85, the years of most extensive sampling, are the basis for most of this paper (see Pearcy and Fisher 1988, for sampling details). A total of 992 quantitative seine sets were made with a 457–495 m seine with 32-mm (stretch measure) mesh that fished to depths of 20–65 m. Sets were made along east-west transects off Oregon and Washington (43°00′N to 48°21′N) at 9.3 km (5 n.mi.) intervals out to about 50 km offshore (Fig. 1). During July 1984, we sampled over a broader area, from northern California (40°32′N) to Vancouver Island (50°26′N).

Trout were identified, measured (fork length, FL), examined for marks, and either released or preserved by freezing at sea. A total of 15 cutthroat and 8 steelhead were tagged with Floy tags and released. In the laboratory ashore, the preserved fish were measured, weighed, scales were removed, stomachs excised, and gonads were examined.

Scales from cutthroat trout and steelhead were collected from an area 1–3 scale rows above the lateral line along the diagonal scale row from the insertion of the dorsal fin (Clutter and Whitesel 1956). Scales were mounted on gummed cards from which acetate impressions were made. The impressions were magnified 88×. All measurements were made in the anterior half of the scale along an axis 20° ventrad to the long axis. Ages of smolts at ocean entrance were estimated by counting the bands of narrowly spaced or broken circuli (interpreted as winter annuli) in the freshwater growth zone of the scale. These freshwater ages are estimates because occasionally "checks," which were difficult to interpret, occurred in the freshwater growth zone and few scales from fish of known freshwater age were available for comparison. The abrupt change from relatively narrowly to widely spaced circuli indicated the transition from freshwater to ocean growth. Subsequent zones of narrowly spaced circuli or resorption on cutthroat trout scales were interpreted as evidence of slow growth from reduced feeding or spawning in freshwater [see Sumner (1962, 1972) and Loch and Miller (1988) for scale interpretations and photographs]. All juvenile steelhead collected were in their first summer in the ocean and had not yet spawned.

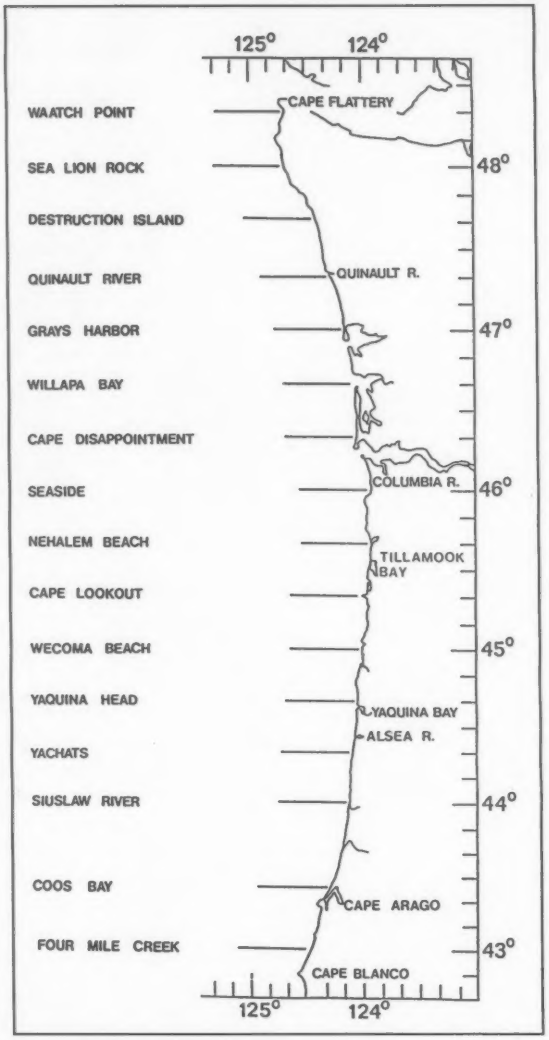

Figure 1
Location of purse seine transect lines off Oregon and Washington.

Size at ocean entrance of cutthroat and steelhead trout caught during their first ocean summer was back-calculated using the method of Lee as described in Carlander (1981):

$$Li = a + ((Lc - a)/Sc) \cdot Si,$$

where Li = FL (mm) at time of ocean entry
Lc = FL (mm) when captured
Sc = total scale radius (mm at 88×)
Si = scale radius at time of ocean entry

a = the y intercept of the regression of FL on scale radius.

The y intercepts (a) for each species were determined from the geometric mean regressions of FL and scale radius (Ricker 1973) from juvenile fish caught in the ocean (cutthroat repeat spawners excluded):

Steelhead

$$FL(mm) = 51.1 + 1.69 \cdot Sc \text{ (mm at } 88\times), \; n = 84, \; r = 0.73, \text{ FL range} = 143\text{–}288 \text{ mm}$$

Cutthroat

$$FL(mm) = 62.1 + 2.26 \cdot Sc \text{ (mm at } 88\times), \; n = 101, \; r = 0.70, \text{ FL range} = 175\text{–}369 \text{ mm}.$$

Sc-FL relationships for both species appeared linear over the length ranges of fish examined. Back-calculation of size at ocean entrance using natural logarithm transformations of FL and Sc (Bartlett et al. 1984, Hooten et al. 1987) produced only very small differences ($\bar{x}$ 1 mm) in back-calculated lengths compared with untransformed data.

We estimated ocean growth for each steelhead and cutthroat trout by subtracting the back-calculated FL at time of ocean entry from the FL at time of capture in the ocean. Growth rates in the ocean of individual fish were estimated from ocean growth back-calculated from scales divided by estimated days in the ocean. To arrive at estimates of time spent in the ocean we used dates of ocean entry corresponding to the beginning, middle, and end of the period of smolt migration into the ocean, yielding several estimates of growth rate for each fish. Seaward migration of cutthroat trout smolts through the Columbia River and coastal Oregon estuaries generally takes place from late March or early April through May (Giger 1972, Loch and Miller 1988, Dawley et al. 1985), with maximum numbers of smolts occurring in the Alsea estuary in the second week of May (Giger 1972). By the end of May very few cutthroat trout smolts were found in the Alsea estuary (Giger 1972). Almost all steelhead smolts passed river kilometer 75 in the Columbia River estuary between 15 April and 15 June, with half the migration completed by the third week in May (Dawley et al. 1985). We used ocean entry dates of 1 April, 1 May, 10 May, and 31 May to estimate growth rates of cutthroat trout, and 15 April, 1 May, and 17 May to estimate growth rates of steelhead. Although ocean entry of steelhead smolts probably continued until about the middle of June, almost all of our catch of steelhead occurred before 15 June.

We also estimated average growth rate of cutthroat trout from the slope of the regression of back-calculated ocean growth on julian date, a method in which no assumptions are made about a precise time of ocean entry. This method was possible because captures of cutthroat in the ocean extended well past the period of smolt entry into the ocean.

Stomach contents were preserved in 10% buffered formalin, transferred to 70% ethanol prior to examination, and weighed to the nearest mg after removal of excess moisture. Contents were examined with a dissecting microscope and were identified to the lowest possible taxon. Total lengths of intact fish prey were measured to the nearest mm. Percent frequency of occurrence in non-empty stomachs (F), percent of the total number of prey organisms (N), and percent of the total wet weight of prey organisms (W) were determined and combined in the Index of Relative Importance (IRI = F(N + W)). Dietary overlaps were calculated from a Percent Similarity Index (= Σ minimum percent weights of taxa in common between two groups of fish). A total of 67 cutthroat (<300 mm in length) and 98 steelhead stomachs were examined from the collections made in 1980–85. The food habits of 48 larger (>300 mm) cutthroat collected during this study were presented by Brodeur et al. (1987a).

Results

Abundance

A total of 163 cutthroat and 134 juvenile steelhead trout were collected during our cruises in 1981–85. These species combined comprised about 3% of our catches of juvenile salmonids (Pearcy and Fisher In press). Cutthroat and steelhead trout were captured from May through August, and occurred in 0–30% and 2–24%, respectively, of the seine sets during these months (Table 1).

Frequencies of occurrence and catches per set of steelhead were generally highest in May and June and were much lower in July and August (Table 1). Steelhead were absent in September of all years. Abundances of cutthroat trout in 1981, the year of most regular sampling, were highest in July and about the same in May, June, and August. Like steelhead, cutthroat trout were absent in September of all years (Table 1).

Distributional trends

In most years, average catches of cutthroat trout were higher in the region off southern Washington and northern Oregon, near the mouth of the Columbia River (Zone B), than off northern Washington (Zone A) or Oregon south of the Columbia River (Zone C) (Table 2). No obvious latitudinal trends were noted

Table 1

Percent frequency of occurrence (FO), mean catch per set (CPS), and number (n) of juvenile cutthroat and steelhead trout caught in purse seine collections, 1981–85, off Oregon and Washington. (S indicates total number of purse seine sets by month.) No steelhead or cutthroat trout were collected in September 1982, 1983, or 1984 (n = 38, 51, and 63 sets, respectively). NS indicates no sets were taken during those months.

	May S = 208			June S = 327			July S = 130			August S = 66		
	FO	CPS	n	FO	CPS	n	FO	CPS	n	FO	CPS	n
Cutthroat												
1981	13	0.29	18	9	0.19	13	30	0.61	41	12	0.21	14
1982	5	0.13	8	14	0.16	9	NS	NS	NS	NS	NS	NS
1983	9	0.13	7	7	0.14	8	NS	NS	NS	NS	NS	NS
1984	NS	NS	NS	6	0.11	7	3	0.05	3	NS	NS	NS
1985	25	0.46	13*	19	0.28	22	NS	NS	NS	NS	NS	NS
Steelhead												
1981	22	0.51	32	15	0.37	25	7	0.07	5	2	0.02	1
1982	24	0.52	32	4	0.04	2	NS	NS	NS	NS	NS	NS
1983	7	0.07	4	3	0.03	2	NS	NS	NS	NS	NS	NS
1984	NS	NS	NS	8	0.12	8	6	0.08	5	NS	NS	NS
1985	18	0.29	8*	6	0.13	10	NS	NS	NS	NS	NS	NS

*Late May and early June sampling off the Columbia R. mouth.

Table 2

Average catch per set of cutthroat/steelhead trout in purse seine sets off Oregon and Washington, during May, June, and July combined, 1981–85 (number of sets in parentheses). NS = no samples.

Zone	1981	1982	1983	1984	1985
A Cape Flattery to Grays Harbor, WA	NS NS	0.04/0.46 (26)	0.05/0.08 (37)	0/0.15 (33)	0/0.10 (20)
B Willapa Bay, WA to Nehalem, OR	0.58/0.54 (111)	0.16/0.31 (45)	0.21/0.03 (33)	0.32/0.16 (25)	0.50/0.15 (54)
C Tillamook Bay to Cape Blanco, OR	0.09/0.02 (86)	0.19/0.17 (47)	0.14/0.47 (43)	0.02/0 (48)	0.23/0.23 (34)
D Extended cruise					
Swiftsure Bank to Winter Harbor, B.C.				0/0 (15)	
Cape Blanco, OR to False Cape, CA				0/0.5 (8)	

for steelhead. Steelhead were captured as far south as northern California during the extended cruise of July 1984.

The highest average catches of both cutthroat and steelhead trout occurred 37.2–46.3 km offshore (Table 3). Low catches of both species were found in the zone closest to shore (<9.3 km). Catches of cutthroat were high 37.2-46.3 km offshore only in May and June 1985, when juvenile coho salmon were also found far offshore (Fisher and Pearcy 1985). In other years highest catches of cutthroat were 9.4–27.8 km offshore, inshore of maximal steelhead catches. The zone of highest average catches for all years was characterized by a mean sea surface temperature of 13.4°C (standard deviation, SD, 1.4), mean surface salinity of 28.6‰ (SD 4.3) and secchi depth of 5.4 m (SD 2.2). The low surface salinities in areas where steelhead and cutthroat trout were abundant indicate the influence of freshwater, often the Columbia River plume. Detailed spatial information on catches is given by Pearcy and Fisher (In press) by cruise.

Table 3

Mean catch per set of cutthroat and steelhead trout and standard deviation at varying distances from the Oregon/Washington coast, 1981–85, giving equal weight to each cruise (15 cruises sampled inshore of 46 km, except 9 cruises at 46.4–55.6 km, and 2 cruises at >55.6 km).

Distance offshore:	km / n.mi.	<9.3 <5	9.4–18.5 5–10	18.6–27.8 10–15	27.9–37.1 15–20	37.2–46.3 20–25	46.4–55.6 25–30	>55.6
Cutthroat	$\bar{x}$	0.09	0.25	0.17	0.15	0.33	0.03	0.10
	SD	0.09	0.26	0.25	0.28	0.61	0.10	0.14
Steelhead	$\bar{x}$	0.03	0.09	0.16	0.23	0.52	0.19	0
	SD	0.06	0.09	0.23	0.36	0.81	0.38	–

Table 4

Release and recapture data for tagged cutthroat and steelhead trout off Oregon and Washington.

Release			Capture		Days between release and recovery	Distance N/S of release (km)	Tagged FL (mm)	Recovered FL (mm)
Date	Location	Code	Date	Location				
Cutthroat								
12 June 85	Yaquina Head	Floy	25 July 85	Siuslaw R.	43	72 S	294	–
18 June 85	Cape Disappoint.	Floy	Fall 85	Umpqua R.	–	290 S	295	–
Steelhead								
27 March–22 May 81	Quinault R., WA	050758	9 June 81	Leadbetter Pt., WA	18–74	85 S		172
4 May 81	Clearwater R., ID	102252	21 May 81	Warrenton, OR	17	9 S		206
14 May 82	Quinault R., WA	051043	31 May 82	Cape Lookout, OR	17	269 S		185
4 May 84	Clearwater R., ID	051335	10 June 84	Cape Disappoint.	37	9 N		194
22 June 83	Cape Disappoint.	Floy	9 Sept. 83	Jones Beach, Col. R.	79	11 S	445	495

Tag recoveries

Two of the cutthroat trout tagged with Floy tags on our cruises in 1985 were recovered by fishermen, one 43 days after release 72 km south of the tagging location and the other 290 km south of the tagging location (Table 4). We also caught four hatchery coded-wire tagged steelhead smolts in the ocean 17–74 days after hatchery release. The two released in the Clearwater River, Idaho, were captured close to the mouth of the Columbia River where they entered the ocean. Two fish released in the Quinault River, Washington, were recovered 85 km and 269 km south of where they entered the ocean. Movements to the south by these two steelhead and the cutthroat trout may have been related to advection of surface waters during the upwelling season (Pearcy and Fisher 1988).

Of the eight maturing steelhead tagged, one (445 mm FL) tagged off Cape Disappointment near the mouth of the Columbia River was recaptured 79 days following its release at 495 mm FL in the Columbia River. Its growth rate between release and recapture was 0.63 mm/day.

Age, lengths, and sex ratios

Of the 110 cutthroat trout with readable scales, 32%, 45%, 19%, and 3% migrated to sea for the first time after one, two, three, and four winters in freshwater (ages 1., 2., 3., and 4.)*, respectively (Table 5). This is a younger age distribution than found by Giger (1972) for wild cutthroat trout from coastal Oregon river systems, but similar to that found by Loch and Miller (1988) in the ocean off the Columbia River mouth. Most of the age 1. cutthroat we caught probably originated from hatcheries (Loch and Miller 1988), including hatcheries on the Columbia River.

Most cutthroat were immature or maturing fish on their first ocean migration (age .0). Only eight fish had scales that showed evidence of reduced growth (a

* Age designation follows that recommended by Koo (1962), and used by others (Godfrey et al. 1975, Hartt and Dell 1986), where the numbers before and after the decimal point refer to winters spent in freshwater prior to first migration to the ocean and winters spent in the ocean, respectively. Ages 1., 2., 3., etc. designate the freshwater age of a fish without reference to its ocean age.

Table 5

Freshwater age* and number of repeat spawners, as determined from scale analysis, and lengths of cutthroat and steelhead trout caught in ocean purse seines off Oregon and Washington.

	Cutthroat					Steelhead			
			Fork length (mm)					Fork length (mm)	
Month	Freshwater age	No. of fish	$\bar{x}$	SD	No. repeat spawners	Freshwater age	No. of fish	$\bar{x}$	SD
May	1.	10	267	46.1	2	1.	35	216	32.5
	2.	12	258	38.7	1	2.	19	185	17.2
	3.	7	279	27.9	1	3.	7	204	17.9
	4.	1	284	—	0	4.	0	—	—
June	1.	13	280	57.4	2	1.	17	209	28.7
	2.	16	282	48.0	1	2.	7	225	36.2
	3.	8	314	16.1	0	3.	2	257	31.8
	4.	2	271	8.5	0	4.	0		
July	1.	10	284	40.9	0	1.	1	260	—
	2.	16	299	34.8	0	2.	1	246	—
	3.	5	336	27.2	1	3.	0		
	4.	0	—	—	0	4.	0		
August	1.	3	321	10.1	0	1.	0		
	2.	6	316	17.9	0	2.	0		
	3.	1	314	—	0	3.	0		
	4.	0	—	—	0	4.	0		
Total		110			8		89		

*See text footnote, p. 701, for explanation of age designation.

winter annulus or spawning check) after initial ocean entrance ("repeat spawners," Table 5). Six of these had apparently made one previous migration from the ocean to freshwater, and two had made two previous trips to freshwater. All of these fish measured 335–380 mm FL except for one 279 mm FL fish. Half of the repeat spawners had first entered the ocean after one winter in freshwater (age 1.). Seven of the eight prior spawners were collected in May or June, probably soon after reentering the ocean.

All juvenile steelhead caught in the ocean were in their first ocean summer (age .0). Of the 89 steelhead that had readable scales, 60%, 30%, and 10% were ages 1.0, 2.0 and 3.0, respectively (Table 5). Ten of 11 steelhead caught with clipped adipose fins, probably denoting hatchery origin, were age 1.0. Since most wild steelhead enter the ocean after two or three winters in freshwater and most hatchery steelhead after only one winter (Chapman 1958, Withler 1966, Pauley et al. 1986), the majority of fish we caught were probably of hatchery origin.

Length ranges were broad for both cutthroat trout and steelhead during each month (1981–85 combined, Fig. 2). This may have resulted from variable size and age of smolts entering the ocean (Loch 1982, Dawley et al. 1982, Bottom et al. 1984, Ward and Slaney 1988) or variable growth rates. During downstream migration, the length ranges of individual hatchery groups of steelhead smolts can be very broad. For example, Dawley et al. (1986) found length ranges of 150–270 mm FL and 110–240 mm FL for two groups sampled in the upper Columbia River estuary.

Back-calculated length at time of ocean entry of cutthroat trout averaged 241 mm FL, but was quite variable (SD 38 mm, $n = 101$, repeat spawners excluded). Age 3.0 fish tended to be larger at time of first ocean entry than younger fish or age 4.0 fish (average back-calculated FL at ocean entry = 231, 239, 264, and 244 mm FL for age 1.0, 2.0, 3.0, and 4.0 fish, respectively). Our average back-calculated lengths at ocean entry for cutthroat trout caught at sea were larger than those back-calculated by Giger (1972) for wild cutthroat of the same age from the Alsea, Nestucca, and Siuslaw Rivers (239 vs. 210 and 264 vs. 239 mm FL for age 2.0 and 3.0 fish, respectively). However, the mean length at ocean entry estimated by Giger for all freshwater age groups and for all three river systems combined (233 mm FL) by Giger was fairly close to our average (241 mm FL).

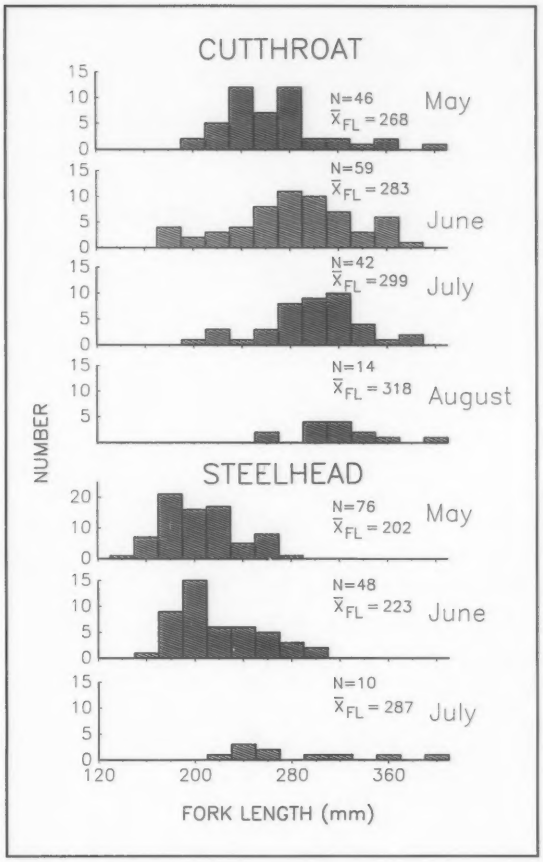

Figure 2
Size-frequency distributions of cutthroat and steelhead trout, by month, 1981–85 combined.

Mean back-calculated FL at time of ocean entry for steelhead was 199 mm (197 mm and 200 mm for fish caught in May and June, respectively) and was quite variable (SD 29 mm, $n = 84$). These estimated lengths at time of ocean entry were similar to the mean lengths of steelhead smolts caught during downstream migration in the Columbia River (~200 mm, Dawley et al. 1985, their figs. 4–10), and similar to those estimated by Narver (1969, 1974) for steelhead smolts in two British Columbia river systems (182 and 190 mm FL), but were larger than mean lengths of all ages of wild smolts from two Washington streams (156 and 165 m FL; Loch et al. 1988).

The mean lengths of both species increased during the summer. This suggests either growth in length during this time period or higher availability of larger fish later in the summer (Loch 1982, Dawley et al. 1982). Mean lengths of cutthroat trout caught in the ocean in July and August (299 and 318 mm FL, respectively) were similar to mean lengths of age 2. and 3. cutthroat trout (305 and 323 mm FL, respectively) caught in coastal Oregon estuaries from July through September on their initial spawning migrations (Giger 1972).

More male than female cutthroat were captured, but fewer male then female steelhead were caught. However, the respective sex ratios of 1.3:1 and 0.7:1 were not statistically different from 1:1 ($p>0.1$, chi-square test). None of the cutthroat trout examined had enlarged testes or ovaries (>1% of body weight), which is expected since cutthroat spawn in the winter-spring period.

Ocean growth

Of cutthroat trout caught in the ocean in May, June, July, and August, 65, 83, 90, and 100%, respectively, showed an ocean growth pattern on their scales. Mean estimated ocean growth rates of cutthroat trout (including fish with and without ocean growth) were 0.47, 0.78, 1.03, and 2.60 mm/day, assuming an ocean entry date of 1 April, 1 May, 10 May, and 31 May, respectively. Since the median date of ocean entry of cutthroat trout smolts is sometime in early May (Giger 1972, Loch and Miller 1988, Dawley et al. 1985), growth rate estimates using 1 May or 10 May as an ocean entry date (0.78 and 1.03 mm/day) are probably closest to the true average growth rate of cutthroat trout in the ocean. Ocean growth rates based on the slope of the geometric mean regression (Ricker 1973) of back-calculated ocean growth and julian date was 1.22 mm/day ($n = 101$, $r = 0.67$), fairly close to the mean growth rates of individual fish assuming early May ocean entry dates.

Almost all juvenile steelhead with readable scales were caught in May and June. Only 30% and 50%, respectively, of the steelhead caught in these two months showed signs of ocean growth on their scales. This suggests that the steelhead caught in May and June were, on average, in the coastal ocean for less time than the cutthroat trout caught in the same months, either because of later ocean entry or rapid migration of steelhead out of coastal waters. Back-calculated ocean growth rates of juvenile steelhead (including fish with and without ocean growth) were 0.21, 0.32, and 1.06 mm/day for assumed ocean entry dates of 15 April, 1 May, and 17 May, respectively. Downstream migration of steelhead smolts in the Columbia River estuary was half completed around the third week in May (Dawley et al. 1985). Consequently, the ocean entry date of 17 May probably gives the best estimate of average growth rate in the ocean (1.06 mm/day). This growth rate was similar to the average

growth rate for cutthroat trout using an early May date of ocean entry. The lack of steelhead caught late in the summer precluded estimating mean growth rate from change in back-calculated ocean growth with time.

Food habits

Cutthroat trout Fishes were by far the dominant prey of juvenile cutthroat trout in terms of frequency, number, and weight. Hexagrammids, scorpaenids, northern anchovy *Engraulis mordax*, and the brown Irish lord *Hemilepidotus spinosus* were the dominant fish taxa identified (Appendix Table 1). One unidentified Pacific salmon, *Oncorhynchus* sp. [81 mm total length (TL)], was found in the stomach of a 221-mm cutthroat trout collected 11.4 km off the mouth of the Columbia River in July 1981. Fishes made up more than 75% of the biomass consumed during all years, but they decreased in importance in the diet as the summer progressed, so that by late summer several other prey taxa such as euphausiids, hyperiid amphipods, and decapod larvae were important. Prey fishes found in cutthroat stomachs averaged 52.5 mm TL (SD 21.8) and ranged from 21 to 101 mm. No significant relation ($n = 46$, $r = 0.30$, $p = 0.16$) was found between the lengths of cutthroat trout and their fish prey.

Steelhead The diet of juvenile steelhead trout was more diverse than that of cutthroat trout. Both arthropods and fishes were important prey items. Prey of steelhead trout ranged from small barnacle larvae and copepods to larger juvenile fishes and squids. Euphausiids, mainly *Thysanoessa spinifera* or *Euphausia pacifica*, accounted for over 75% of the total IRI for all years combined (Appendix Table 1). Fishes were more important, however, on a weight basis making up about 60% of the total biomass consumed. Juvenile rockfishes (*Sebastes* spp.), sandlance *Ammodytes hexapterus*, brown Irish lord *Hemilepidotus spinosus*, and greenlings (*Hexagrammos* spp.) were the dominant fish taxa identified. With the exception of barnacle cypris larvae and hyperiid amphipods which were quite numerous in stomachs collected at several stations, all other prey taxa were relatively unimportant. No relationship between predator and fish prey size was found ($n = 38$, $r = 0.19$, $p = 0.25$). However, steelhead, which had a smaller mean length than cutthroat trout, consumed a smaller mean size ($\bar{x}$ 35.9 mm TL, SD 16.6 mm) and size range (7–72 mm) of prey fishes than cutthroat trout.

The relative proportions by weight of the major prey categories varied substantially among the years sampled. Usually, fishes contributed the majority of the weight to the diet, but during the relatively strong upwelling years of 1982 and 1985 (Fisher and Pearcy 1988) euphausiids were more important. The largest number of prey categories occurred in steelhead and cutthroat stomachs during the relatively weak upwelling summers of 1981 and 1984.

The Percent Similarity Index between cutthroat trout and steelhead was 39% for all cruises combined.

Discussion

Cutthroat and steelhead trout have evolved contrasting migratory behavior in the ocean. Both species were absent in purse seine catches during September of their first summer in the ocean (Miller et al. 1983, Loch and Miller 1988; this paper), apparently because they migrated out of the coastal ocean. Cutthroat return to estuaries and freshwater streams from mid- to late summer (Giger 1972, Loch 1982), whereas most steelhead migrate far offshore during their first summer in the ocean (Hartt and Dell 1986).

Although some aspects of the life histories of cutthroat and steelhead trout are similar, their ecologies in marine waters differ. Steelhead commonly spend 2–3 years in the ocean and attain a large size before initiating their spawning migrations to freshwater. Some, however, return after only one full year in the ocean, and some return, though usually do not spawn, after several months in the ocean (Everest 1973). Apparently anadromous cutthroat trout return to freshwater after only a few months in coastal waters and rarely overwinter at sea. Giger (1972) did not identify any coastal cutthroat that had overwintered in the ocean, based on analyses of circuli patterns from scales of fish returning to coastal rivers of Oregon. Fish that migrated to sea in the spring invariably returned to freshwater in the summer or fall of the same year. Similarly, Armstrong (1971), Jones (1982) and Loch, and Miller (1988) did not report any cutthroat that spent an entire year in the ocean. J. Johnston (Wash. Dep. Wildl., Olympia, pers commun. 8 March 1990) found a few cutthroat trout in Hood Canal, WA, during February and March, fish that evidently overwintered in marine waters. Most cutthroat spawn after their return to freshwater, but according to Johnston (1982) a large percentage of the Columbia River, Puget Sound, British Columbia, and Alaska stocks of cutthroat overwinter but do not spawn in freshwater after their first summer in the ocean. Jones (1977) reported that less than 50% of the cutthroat migrating into Petersburg Creek in southeast Alaska were approaching sexual maturity. In some instances, coastal cutthroat may migrate downstream but not into the ocean. Smolts from the Cowlitz River in Washington may remain in the Columbia River estuary for a year (Tipping 1981 as cited by Johnston 1982), and some adults that

return to spawn in Sand Creek, OR, and Prairie Creek, CA, had no ocean growth on their scales (Sumner 1972, DeWitt 1954). Tomasson (1978) thought that coastal cutthroat did not migrate in large numbers beyond the Rogue River estuary.

Because coastal cutthroat only spend several months in the ocean, it is assumed that they inhabit waters close to the coast and not far from their homestream (Giger 1972). Johnston (1982) observed that anadromous cutthroat usually frequented waters less than 3 meters in depth in Puget Sound and that migration of tagged wild cutthroat did not extend much beyond 50 km from the home stream. However, cutthroat were caught by Loch and Miller (1988) up to 31.5 km offshore and within the Columbia River plume between Tillamook Bay, OR, and Willapa Bay, WA, suggesting more extensive offshore movements. Sumner (1972) also thought that cutthroat originating from the Columbia River basin may traverse along the coast within the Columbia River plume. Our data also suggest that some cutthroat undertake substantial movements along the coast (>250 km) and are found as far offshore (37–46 km) as the more oceanic steelhead smolts during the summer. One fish was caught 66 km offshore. Thus some individuals may reside far offshore along an open coast, as opposed to staying close to shore as they presumably do in protected inlets like Puget Sound (Johnston 1982). Straying of returning sea-run hatchery cutthroat trout is common (Bulkley 1966, Giger 1972, Jones 1977). Giger (1972) reported straying of marked hatchery cutthroat between the Nestucca, Siuslaw, and Alsea Rivers of the central Oregon coast. Most of the strays were recovered in rivers south of the river of release, possibly the result of advection by coastal currents during the early summer period of ocean residence, similar to that seen for coho salmon (Pearcy and Fisher 1988).

Giger (1972) noted a non-random distribution in the number of cutthroat smolts and kelts in seine samples in the Alsea estuary during the spring and "large schools" of sea-run fish in estuaries in the fall. He thought that anadromous cutthroat trout formed schools while at sea. However, we found no evidence of schooling from our limited ocean catches. Most cutthroat were caught singly. To our knowledge, schooling of cutthroat or steelhead trout in the ocean has not been documented.

Steelhead migrate long distances into oceanic waters and are widely distributed in the North Pacific Ocean based on catches of marked and unmarked fish (Sutherland 1973; Pearcy and Masuda 1982, 1987; Okazaki 1983; Hartt and Dell 1986; Light et al. 1988). Miller et al. (1983) found that juvenile steelhead caught in purse seines between Tillamook Bay and Willapa Bay occurred farther offshore than juvenile coho or chinook salmon and migrated out of the coastal sampling area early in the summer. Purse seining and tagging studies by Hartt and Dell (1986) from Cape Flattery, WA, to the Aleutian Islands clearly showed that juvenile steelhead migrate directly offshore rather than along a coastal belt where other juvenile salmonids typically migrate. Recovery of steelhead during their first summer in the ocean in the Gulf of Alaska confirms rapid migrations of some fish into oceanic waters far from land. Pearcy and Masuda (1982) report on a steelhead captured over 1600 km from land only a few months after its initial ocean entry.

These conclusions of immediate migrations of steelhead offshore and into subarctic waters of the North Pacific after ocean entry, and residence in oceanic waters during their first winter in the ocean, do not apply to all steelhead. Most steelhead from the Rogue River in Oregon (the "half-pounder" runs) return to freshwater after only a few months following their initial migration to the ocean (Everest 1973), and likely do not migrate very far in the ocean. The recovery of marked Rogue River summer steelhead south of the Rogue River (Everest 1973), and the rarity of marked steelhead originating from streams south of Cape Blanco in waters to the north of Cape Blanco in our catches, suggest that these steelhead from the southern extremity of their range may not migrate to the north after ocean entry. This conclusion is supported by the high seas distribution of tagged steelhead. Although 9 tagged steelhead from California and 11 from Oregon streams have been recovered north of 45°N in the northeastern Pacific, only 3 fish with coded-wire tags from California have been recovered at sea of the over 1 million coded-wire tagged steelhead released between 1980 and 1985, and only one was caught north of California (Light et al. 1988, Pacific States Marine Fisheries Comm. unpubl.). Possibly southern steelhead reside in the strong upwelling zone off northern California and southern Oregon (Bakun 1975).

The feeding habits of juvenile steelhead and cutthroat trout in estuaries and in coastal waters are similar. Both species feed intensively on gammarid amphipods and insects in estuaries on their initial migration to the sea, but steelhead smolts also eat the benthic mollusk *Corbicula* (Loch 1982, McCabe et al. 1983, Bottom et al. 1984). During their early residence in waters along the open coast, cutthroat trout feed primarily on fishes (Armstrong 1971, Fresh et al. 1981, Brodeur et al. 1987a, Loch and Miller 1988, this paper). We found that steelhead trout also consumed fish but had a more varied diet than cutthroat trout. Euphausiids and other crustaceans were important in the diet of steelhead trout, especially during the strong upwelling years of our study when euphausiids may have been abundant (Brodeur 1986). Many prey species identified in the

diets of the trout species (juvenile rockfishes, hexagrammids, anchovy, *Cancer* spp. megalopae, and insects) are commonly found in the neustonic layer (Brodeur et al. 1987b, Shenker 1988) which suggests that these trouts feed in surface waters. The occurrence of a juvenile salmon in the diet of juvenile cutthroat is noteworthy since larger individuals (>300 mm) of this species were identified as one of the few fish predators on juvenile salmonids among the 20 species of nekton examined from these same purse seine catches (Brodeur et al. 1987a).

Dietary overlap of 39% between cutthroat and steelhead trout based on percent similarity was higher than the overlap values between these species of trout and the juveniles of four species of salmon caught in purse seines, with two exceptions. The highest overlap values were between cutthroat trout and juvenile chinook salmon (49%) because of the common utilization of fishes in the diet, and between juvenile steelhead trout and juvenile sockeye salmon (43%) because of the common occurrence of euphausiids.

The average growth rate of cutthroat trout in the ocean based on our scale analysis was 0.8 and 1.0 mm/day (based on 1 May and 10 May dates of ocean entry, respectively) and 1.2 mm/day (based on change in back-calculated ocean growth with time). These estimates are similar to the growth rates of about 1.0 mm/day for age 2. wild cutthroat and 0.9 mm/day for hatchery cutthroat, assuming a 3-month ocean residence (Giger 1972) and 0.7–0.8 mm/day for fish after their first 5–6 months in the ocean (Sumner 1962). Johnston (1982) reported an average growth rate of 1.0 mm/day during the time spent at sea for cutthroat trout stocks from the Columbia River, coastal rivers, and Puget Sound rivers. Our average growth rate for steelhead of 1.1 mm/day (based on a 17 May date of ocean entrance) is similar to that for cutthroat trout. It is about the same as the average ocean growth of 1.3 mm/day calculated by Everest (1973), the 0.8 mm/day estimated by K. Kenaston (Oreg. Dep. Fish Wildl., Corvallis, pers. commun. 16 June 1989) for summer-run steelhead "half-pounders" of the Rogue River, and the 1.5 mm/day estimated for first-year ocean growth of steelhead from Vancouver Island (Hooten et al. 1987). Data on ocean growth of steelhead during their first year in the ocean is also provided by recovery of fish with coded-wire tags. These include growth rates of about 1.0 mm/day for a fish caught in the Gulf of Alaska, based on the mean size of the same tag code of steelhead smolts when caught about 60 days earlier in the Columbia River (Pearcy and Masuda 1982), and growth rates of 0.7, 1.0, and 1.2 mm/day for coded-wire tagged steelhead recovered 198, 186, and 173 days, respectively, after release (Pacific States Marine Fisheries Comm. unpubl.). Lengths at release were estimated from release weight using the length-weight relationships for steelhead smolts given by Everest (1973). The average growth rate of steelhead during their first full year in the ocean was about 1.0 mm/day for fish returning to California streams (calculated from data in Shapovalov and Taft 1954), 0.6 mm/day for fish caught on the high seas (Sutherland 1973), and 0.85 mm/day for fish from the Keogh River, British Columbia (Ward and Slaney 1988). These estimates suggest fairly similar growth rates for both cutthroat and steelhead trout during early ocean life. Apparently cutthroat trout are small when they return to spawn because they spend less time in the ocean, not because of an inherently lower growth rate.

If coastal cutthroat trout have the potential for a large increase in size during ocean life, why do they curtail marine growth by returning to freshwater each winter rather than remaining in the ocean for several years like most steelhead trout? We present three hypotheses for the adaptive value of this behavior.

Early maturation of cutthroat trout, after only a few months in the ocean, may have evolved as a response to low survival (Cole 1954), either in the ocean or freshwater, especially if postreproductive survival is low after the age at first breeding (Schaffer 1974). Cutthroat trout do not appear to have distinctly lower ocean survival than steelhead, however, based upon the reports in literature. Giger (1972) states that coastal cutthroat exhibited comparatively high rates of survival during summer periods of ocean residence between spawnings. He estimated ocean survival rates of 20–40% for hatchery cutthroat smolts between release in the spring and return in the fall, and survival rates of 14–39%, 17–35%, and 12–25% between first and second, second and third, and third and fourth spawnings, respectively, based on trap or net catches of fish returning to four Oregon coastal streams. Sumner (1962) estimated that 17–50% of coastal cutthroat trout survived between successive spawnings, and Jones (1978) reported marine survival of 17%. Tomasson (1978), on the other hand, noted that 92% of the fish returning to the Rogue River were first migrants, suggesting low survival of repeat spawners, and Michael (1983, 1989) reported marine survival rates of 2–20% between smolt outmigration and first return to freshwater for coastal cutthroat trout.

Cutthroat survival to an ocean age of 2, the age when many steelhead trout return for their initial spawning (Withler 1966, Shapovalov and Taft 1954, Chapman 1958), is about 5% (assuming 20% survival from smolt to first spawning and 25% survival from first to second spawning, based on Giger's estimates), a value which is close to the average for smolt to adult return for steelhead (Bley and Moring 1988), but less than the mean ocean survival of 16% based on maiden-run fish

given by Ward and Slaney (1988). Thus survival rates to ocean age 2 of these two species appear to be roughly similar, as is survival of repeat spawners of cutthroat trout and steelhead trout (Giger 1972, Withler 1966, Ward and Slaney 1988). Lower ocean survival or lower postreproductive survival of cutthroat trout than steelhead may not be a cogent explanation for cutthroat trout spawning at an early age and small size.

The second hypothesis is that small size at maturity in cutthroat trout relative to steelhead trout may have evolved as a result of the distance and rigor of spawning migrations. Schaffer and Elson (1975) concluded that the mean age of first spawning of Atlantic salmon increased with the difficulty of upstream migration, as estimated by the distance ascended into freshwater. Coastal cutthroat rarely penetrate inland more than 160 km (Johnston 1982), and hence may not need the swimming performance or energy reserves required for the long and arduous upstream migrations that some steelhead undertake at the time of maturity.

Finally, the small size at maturity attained by cutthroat trout may permit utilization of small, shallow tributaries for spawning and rearing where interspecific competition with other anadromous salmonids is reduced. Small streams are known to be important spawning and rearing areas of cutthroat trout (DeWitt 1954, Needham and Gard 1959, Lowry 1965, Johnston 1982, Trotter 1989). Sea-run cutthroat trout generally spawn in tributaries with a lower velocity and shallower depth than steelhead (Hunter 1973). Hartman and Gill (1968) reported that where both anadromous cutthroat trout and steelhead were sympatric, juvenile cutthroat were predominant in headwater tributaries and steelhead in larger river reaches. Cutthroat trout are behaviorally subordinate to steelhead and coho salmon in agonistic encounters (Nilsson and Northcote 1981, Glova 1986, Griffith 1988) and their populations appear to be suppressed by competition from anadromous salmonids (R. House, Unpubl.). The lack of morphological specialization of cutthroat trout to either fast or slow water may be another reason why this species is dominated by coho salmon and steelhead in areas of sympatry (Bisson et al. 1988). Anadromous cutthroat are known to penetrate, spawn, and rear farther into a watershed than steelhead trout (Michael 1983), sometimes above natural falls or log jams (Mitchell 1988; R. House, Unpubl.) that were considered to be barriers to anadromous salmonids (see Michael 1983). Therefore, small size at maturity may be adaptive by allowing anadromous cutthroat trout to spawn and rear in numerous small tributaries of coastal streams where other salmonids are absent or less abundant.

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Appendix Table 1

Percent frequency occurrence (F), percent number (N), percent weight (W), and percent index of relative importance (IRI) of food items in juvenile steelhead and cutthroat trout stomachs for all years combined. Values in parentheses are summaries by major taxonomic categories.

	Steelhead trout				Cutthroat trout			
Prey taxa	F	N	W	IRI	F	N	W	IRI
Cnidaria								
Velella velella	1.1	<0.1	0.1	<0.1	—	—	—	—
Siphonophora								
Unidentified	1.1	<0.1	<0.1	<0.1	—	—	—	—
Annelida								
Tomopteris septentrionalis	1.1	<0.1	<0.1	<0.1	—	—	—	—
Tomopteris spp.	1.1	<0.1	<0.1	<0.1	—	—	—	—
Mollusca								
Gastropoda								
Limacina helicina	1.1	4.8	0.1	0.1	3.2	0.5	0.1	<0.1
Cephalopoda								
Loligo opalescens	1.1	<0.1	<0.1	<0.1	—	—	—	—
Unidentified	1.1	<0.1	0.1	<0.1	—	—	—	—
Arthropoda								
Copepoda	(4.2)	(4.0)	(0.1)					
Neocalanus cristatus	1.1	0.1	<0.1	<0.1	—	—	—	—
Epilabidocera longipedata	1.1	<0.1	<0.1	<0.1	—	—	—	—
Euchaeta elongata	1.1	3.9	<0.1	0.1	—	—	—	—
Unidentified	1.1	<0.1	<0.1	<0.1	—	—	—	—
Cirripedia								
Unidentified cypris	18.1	9.6	0.5	3.4	—	—	—	—
Unidentified remains	6.4	0.4	1.1	0.2	—	—	—	—
Isopoda								
Gnorimosphaeroma oregonensis	1.1	0.1	<0.1	<0.1	—	—	—	—
Idotea fewkesi	—	—	—	—	1.6	<0.1	0.1	<0.1
Amphipoda	(29.5)	(5.1)	(1.6)					
Caliopius laeviusculus	1.1	<0.1	<0.1	<0.1	—	—	—	—
Unidentified Gammaridea	1.1	<0.1	<0.1	<0.1	—	—	—	—
Hyperia medusarum	3.2	0.1	0.3	<0.1	—	—	—	—
Hyperoche medusarum	21.3	2.2	1.0	1.3	6.5	0.7	0.1	0.1
Themisto pacifica	3.2	2.7	<0.1	<0.1	1.6	<0.1	0.1	<0.1
Brachyscelus crusculum	1.1	<0.1	0.1	<0.1	—	—	—	—
Unidentified Hyperiidea	2.1	0.1	0.1	<0.1	1.6	0.2	<0.1	<0.1
Caprella incisa	1.1	<0.1	<0.1	<0.1	—	—	—	—
Euphausiacea	(67.4)	(54.1)	(32.7)		(24.2)	(16.0)	(2.0)	
Euphausia pacifica	43.6	8.3	12.0	16.4	8.1	0.5	0.4	0.2
Nematoscelis difficilis	—	—	—	—	1.6	0.1	0.1	<0.1
Thysanoessa spinifera	50.0	43.9	19.8	58.8	9.7	9.4	0.2	2.4
Thysanoessa longipes	1.1	1.3	<0.1	<0.1	—	—	—	—
Nyctiphanes simplex	1.1	0.1	<0.1	<0.1	—	—	—	—
Unidentified furcilia	1.1	<0.1	<0.1	<0.1	—	—	—	—
Unidentified	12.8	0.5	0.9	0.3	8.1	6.0	1.3	1.5

Appendix Table 1 (continued)

Prey taxa	Steelhead trout F	N	W	IRI	Cutthroat trout F	N	W	IRI
Euphausiacea (continued)								
Decapoda	(14.7)	(5.6)	(1.9)		(17.7)	(4.9)	(1.4)	
Crangon spp. zoea	–	–	–	–	1.6	0.5	<0.1	<0.1
Pagurus spp. zoea	–	–	–	–	1.6	<0.1	<0.1	<0.1
Pagurus spp. megalopae	–	–	–	–	1.6	0.5	<0.1	<0.1
Porcellanidae megalopae	–	–	–	–	1.6	0.5	<0.1	<0.1
Pugettia producta zoea	–	–	–	–	3.2	0.1	<0.1	<0.1
Cancer antennarius megalopae	2.1	<0.1	<0.1	<0.1	1.6	0.1	<0.1	<0.1
Cancer magister megalopae	8.5	0.5	1.4	0.3	12.9	2.9	1.3	1.4
Cancer oregonensis megalopae	5.3	2.4	0.4	0.3	3.2	0.1	<0.1	<0.1
Cancer spp. zoea	2.1	2.7	<0.1	0.1	1.6	<0.1	<0.1	<0.1
Pinnotheridea megalopae	–	–	–	–	1.6	<0.1	<0.1	<0.1
Unidentified larvae	1.1	<0.1	<0.1	<0.1	1.6	<0.1	<0.1	<0.1
Insecta	(8.4)	(0.2)	(0.2)		(8.1)	(1.2)	(0.8)	
Choristoneura occidentalis	1.1	<0.1	<0.1	<0.1	–	–	–	–
Hymenoptera	–	–	–	–	3.2	0.7	0.6	0.1
Coleoptera	1.1	<0.1	<0.1	<0.1	–	–	–	–
Hemerobiidae	1.1	<0.1	<0.1	<0.1	–	–	–	–
Diptera	2.1	<0.1	<0.1	<0.1	1.6	<0.1	<0.1	<0.1
Unidentified	5.3	0.1	0.1	<0.1	6.4	0.5	0.2	0.1
Chordata								
Osteichthyes	(70.5)	(16.0)	(61.4)		(87.1)	(76.2)	(95.1)	
Clupea harengus pallasi	4.2	0.1	2.4	0.2	–	–	–	–
Engraulis mordax	–	–	–	–	9.7	1.3	7.8	2.3
Allosmerus elongatus	1.1	0.1	3.7	0.1	–	–	–	–
Spirinchus thaleichthys	–	–	–	–	1.6	0.1	3.7	0.2
Osmeridae	1.1	<0.1	0.1	<0.1	3.2	0.1	6.6	0.6
Oncorhynchus sp.	–	–	–	–	1.6	0.1	2.0	0.1
Sebastes flavidus	–	–	–	–	1.6	0.1	1.4	0.1
Sebastes jordani	1.1	<0.1	1.2	<0.1	–	–	–	–
Sebastes spp.	21.3	0.4	22.5	9.0	11.3	5.0	7.9	3.8
Anoplopoma fimbria	2.1	0.1	0.1	<0.1	1.6	<0.1	0.9	<0.1
Hexagrammos decagrammus	2.1	0.1	1.8	0.1	9.7	0.7	16.7	4.3
Hexagrammos spp.	4.3	0.1	4.9	0.4	8.1	27.7	7.6	7.3
Ophiodon elongatus	3.2	<0.1	0.9	0.1	3.2	0.1	0.9	0.1
Agonidae	1.1	1.3	<0.1	<0.1	–	–	–	–
Hemilepidotus spinosus	7.4	0.2	4.3	0.6	12.9	0.9	7.4	2.7
Scorpaenichthys marmoratus	3.2	0.1	0.1	<0.1	4.8	4.8	5.2	1.2
Cottidae	3.2	5.3	0.1	0.3	–	–	–	–
Ammodytes hexapterus	10.6	1.6	3.3	1.0	9.7	0.6	2.9	0.9
Ronquilus jordani	1.1	1.3	0.1	<0.1	–	–	–	–
Citharichthys sordidus	1.1	<0.1	0.4	<0.1	–	–	–	–
Psettichthys melanostictus	1.1	0.1	0.8	<0.1	–	–	–	–
Unidentified larvae	13.8	0.5	2.4	0.7	4.8	0.3	0.5	0.1
Unidentified juveniles	8.5	1.5	4.4	0.9	16.1	0.8	10.6	4.7
Unidentified remains	24.5	3.1	7.9	5.0	54.8	33.6	13.0	65.6
Plant material	2.1	<0.1	0.1	<0.1	1.6	<0.1	0.5	<0.1
Number of stomachs examined		98				67		
Number of empty stomachs		4				5		
Mean fork length (mm)		213.4				254.5		
Fork length range (mm)		158–294				162–298		

Genetic Variation in Highly Exploited Spiny Lobster *Panulirus marginatus* Populations from the Hawaiian Archipelago

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Abstract.– Spiny lobsters *Panulirus marginatus* from the Hawaiian Archipelago have undergone heavy fishing pressure since 1980 and have experienced increases in asymptotic length and decreases in mean length at onset of egg production. Prior to the expansion of the fishery, allozyme variation was surveyed, and populations were found to be polymorphic at seven loci. In 1987 we collected spiny lobsters from two of the previously sampled locations (Necker Island and Maro Reef) to test for significant changes in population structure or level of genetic variability. No significant changes through time were found at five of the seven loci. Significant differences were detected at *Est3* and *EstD*; however, frequencies at esterase loci have been previously shown to fluctuate through time. Observed number of allelic classes and observed heterozygosities have remained unchanged. The data suggest that no change in the amount of variability has occurred in spiny lobster since the expansion of the fishery.

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Commercial trapping for the spiny lobster *Panulirus marginatus* in the northwestern Hawaiian Islands began in 1976 shortly after research cruises documented the resource in abundance. Two banks, Necker Island and Maro Reef, have been most heavily fished since the beginning of the fishery. In 1986 and 1987 research cruises repeated the earlier sampling at Necker Island and Maro Reef by trapping at the same sites on each bank with the same gear to document any changes that had occurred in density, population, and genetic parameters (Polovina 1989). The repeat sampling documented substantially reduced lobster densities as indicated by catch rates, which in 1986–87 were 37% and 68% of their 1977 levels at Necker Island and Maro Reef, respectively (Polovina 1989). A statistically significant ($P<0.05$) increase in the asymptotic lengths and decreases in the mean lengths at onset of egg production occurred between the 1977 and 1986–87 sampling at both locations (Polovina 1989).

While changes in these population parameters could be due to density-dependence relationships, some type of genetic change also may have occurred from selection induced by the fishing pressure (Nelson and Soulé 1987). For example, the fishery harvests lobsters at about the size the females first begin producing eggs. It is estimated that spiny lobster enter the fishery at 3.1 years of age and that the mean age females begin producing eggs is 2.5 years (Polovina 1989). Thus, heavy fishing pressure may select for female lobsters that sexually mature at a smaller size. Reduction in the total amount of genetic diversity or changes in the stock structure of the exploited populations are also potential results of intense fishing pressure (Allendorf et al. 1987). These latter types of genetic changes can often be monitored through allozyme analyses (Nelson and Soulé 1987), and are the subject of this paper.

Spiny lobsters from seven localities in the Hawaiian Archipelago were collected between 1978 and 1980, prior to the expansion of the commercial fishery, and analyzed for allozyme variation by Shaklee and Samollow (1984). Although overall levels of variation were quite low, they observed polymorphism at 7 of the 46 loci examined. However, no clear pattern of genetic differentia-

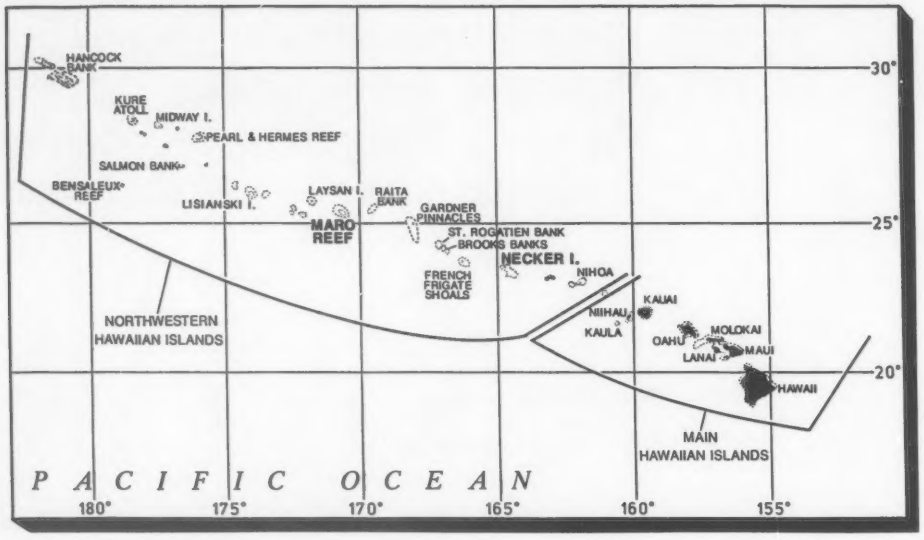

Figure 1
Location of Maro Reef and Necker Island within the Hawaiian Archipelago.

tion among populations was detected, and they concluded that a single panmictic stock of spiny lobster exists throughout the Hawaiian Archipelago.

Our objective was to reexamine allozyme variation at those seven loci to determine if fishing pressure since 1980 affected population structure or genetic variability. During 1987, new collections of spiny lobsters from two of the same localities in the northwestern Hawaiian Islands (Maro Reef and Necker Island) were made. These two sites represent the mainstay of the commercial fishery. They are the most productive banks, have been fished the longest, and annually receive the greatest fishing pressure.

Analysis showed that the observed number of allelic classes and observed heterozygosity have remained essentially unchanged between 1978 and 1987. These data provide no evidence that population bottlenecks have occurred. Fishing pressure since 1980 has not reduced the genetic variability as detected by protein electrophoresis in spiny lobster from either of these two sites in the northwestern Hawaiian Islands.

Methods and materials

Muscle and digestive gland from 200 specimens from Maro Reef and Necker Island (Fig. 1) were collected, frozen onboard ship, and shipped frozen to the laboratory for analysis. Upon receipt, tissues were subsampled for electrophoresis and stored at −80°C for up to 4 weeks while analysis was completed.

Electrophoretic methods generally followed May et al. (1979) and Shaklee and Samollow (1984) to facilitate comparison. Samples were analyzed for the products of seven loci previously identified as polymorphic: *Est3*, Esterase, E.C. 3.1.1.–; *EstD* (*Umb*), Esterase, E.C. 3.1.–.–, resolved with 4-methylumbelliferyl acetate; *Gpi*, glucosephosphate-6-isomerase, E.C. 5.3.1.9; *Mpi*, mannose-6-phosphate isomerase, E.C. 5.3.1.8; *Pgm*, phosphoglucomutase, E.C. 5.4.4.2; *Tpep1,2* (*Pep-1,2*), tripeptidase aminopeptidase, E.C. 3.4.–.–, resolved with L-leucyl-L-leucyl-L-leucine. However, in contrast to the methods of Shaklee and Samollow (1984) who used horizontal and vertical gels, all analyses were performed on horizontal starch gels. *Tpep1* was resolved on an additional buffer, amine-citrate gel and tray buffer, pH 6.9 (Clayton and Tretiak 1972).

The electrophoretic data were analyzed using BIOSYS-1 (Swofford and Selander 1981). Allelic classes followed those of Shaklee and Samollow (1984), who pooled alleles into f(fast), m(medium), and s(slow) classes for numerical analyses. Pooling was required in their study and ours because many alleles were too rare to include in the statistical tests. Actual mobilities observed were also recorded.

Comparisons between the 1978–80 and 1987 data sets for each reef were performed using a chi-square contingency analysis based on the number observed in

Table 1

Allele frequencies for seven polymorphic loci in the spiny lobster *Panulirus marginatus*. Data from 1978–80 are those of Shaklee and Samollow (1984). Alleles are identified by relative mobility classes assigned by Shaklee and Samollow (1984). Actual mobilities observed in this study are also given. Numbers of individuals successfully scored are given in parenthesis.

	Est3			*EstD*			*Gpi*			
Location and date	f	m 100	s 93	f	m 100	s	f 100	m 88	s 66	ff 145
Maro Reef										
1978–80	0.003	0.957 (386)	0.040	0.001	0.988 (340)	0.010	0.959	0.039 (320)	0.002	—
1987	—	0.968 (174)	0.032	—	1.000 (199)	—	0.970	— (198)	0.028	0.003
Necker Island										
1978–80	—	0.971 (666)	0.030	0.011	0.980 (533)	0.008	0.966	0.033 (535)	0.001	—
1987	—	0.992 (194)	0.008	—	1.000 (200)	—	0.955	0.002 (200)	0.020	0.022

	Mpi		*Pgm*			*Tpep1*		*Tpep2*		
	f 101	f+s 96, 100	f 200	m 100	s −33 −66	f 100	s 66	f ***	m 100	s 89
Maro Reef										
1978–80	0.011	0.989 (418)	0.007	0.984 (345)	0.009	0.725	0.275 (142)	—	0.988 (335)	0.012
1987	0.005	0.995 (193)	0.003	0.977 (198)	0.020	0.768	0.232 (179)	0.006	0.975 (180)	0.019
Necker Island										
1978–80	0.007	0.993 (649)	0.007	0.976 (558)	0.017	0.785	0.215 (142)	0.001	0.984 (425)	0.015
1987	0.003	0.998 (188)	—	0.985 (200)	0.014	0.768	0.232 (144)	—	0.980 (176)	0.020

each allelic class. Shaklee and Samollow (1984) found no heterogeneity between year classes for any loci except *EstD*, and thus they report pooled frequencies. They provide annual frequency estimates for *EstD* for 1979 and 1980.

We also compared the 1987 data sets from Maro Reef and Necker Island using chi-square contingency analysis.

Results

Allozyme analysis

All loci previously observed to be polymorphic were also found to be variable in the new samples, with the exception of *EstD* (Table 1). Allele classes observed by Shaklee and Samollow (1984) and not observed in this study were *Est3(f)*, *EstD(f)*, and *EstD(s)*. We observed *Gpi(145)* in both populations; this allele was not previously reported. Additionally, when analyzing *Tpep1* allozymes, we detected a *Tpep3(94)* allele in a single individual from Maro Reef which was not observed previously. Isozyme patterns agreed with descriptions provided in the earlier study. There were no indications of non-genetic variation at the esterase or any of the other loci.

Genotypic frequencies at all loci fit the expectation of Hardy-Weinberg equilibrium with the exception of *Est3* in Maro Reef ($P = 0.041$) and *Mpi* in both populations. *Mpi* has an unusual distribution of alleles between the two sexes (Shaklee 1983). Males always carry at least one slow allele, while females rarely have this variant. The common and slow variant alleles were pooled for the statistical analyses, and only the frequency of the fast allele is reported. With pooling, a test for fit to Hardy-Weinberg is possible, and no significant deviation from Hardy-Weinberg was observed.

Table 2
Average per locus and mean heterozygosity over all loci for spiny lobster *Panulirus marginatus* from Maro Reef and Necker Island.

Location and date	*Est3*	*EstD*	*Gpi*	*Mpi*[1]	*Pgm*	*Tpep1*	*Tpep2*	Mean[2]
Maro Reef 1987	0.061	0.000	0.059	0.381	0.045	0.356	0.049	0.021
Necker Island 1987	0.015	0.000	0.087	0.477	0.030	0.389	0.039	0.023
Hawaiian Archipelago 1978–80[3]	0.059	0.032	0.076	0.374	0.042	0.370	0.026	0.021

[1]Sex restricted allele distribution (Shaklee 1983).
[2]1987 estimate assumes monomorphism at the 39 additional loci surveyed by Shaklee and Samollow (1984).
[3]From Shaklee and Samollow (1984).

Chi-square analyses

Contingency chi-square analyses were performed between the two newly sampled collections at each of the polymorphic loci. Because of their low frequencies, all variant alleles at each locus were pooled into one class. Significant heterogeneity between Necker Island and Maro Reef was observed for *Est3* ($\chi^2 = 5.61$, df = 1, $P<0.020$).

Contingency chi-square analyses were also performed between the data gathered in this study and those of Shaklee and Samollow (1984) at each of the polymorphic loci. Significant heterogeneity was observed between the Necker Island 1987 and 1979–80 collections at *Est3* ($\chi^2 = 5.86$, df = 1, $P<0.025$).

Shaklee and Samollow (1984) reported fluctuating frequencies over years at the *EstD* locus and concluded that the 1980 samples represented a cohort with an unusual frequency. Therefore, we tested for heterogeneity between our data and the 1979 and 1980 *EstD* data separately. Both Maro Reef and Necker Island were significantly different for the 1980 comparison (Maro Reef, $\chi^2 = 9.71$, df = 1, $P<0.005$; Necker Island, $\chi^2 = 15.42$, df = 1, $P<0.001$). The Necker Island 1987 data were significantly different from the 1979 data ($\chi^2 = 6.10$, df = 1, $P<0.02$); the Maro Reef data were not significantly different.

Number of allelic classes

The total number of observed alleles at all sampled loci can also be used as an indicator of overall variability. Shaklee and Samollow (1984) observed a total of 18 different allelic classes in both the Maro Reef and Necker Island collections; we observed, for the same loci, 16 and 15 classes, respectively (Table 1). Although three classes (with frequencies of 0.010 or less) detected earlier were not observed in this study, two new alleles were observed.

It is also important to note the persistence of low-frequency allelic classes. *Gpi(s)*, *Pgm(f)*, and *Pgm(s)* were present in the 1978–80 Maro Reef collections at frequencies of 0.009 or less; all were present in the 1987 collection. *Gpi(s)* and *Mpi(f)* were present in the 1978–80 Necker Island collection at frequencies of 0.007 or less; both were present in the 1987 collection.

Heterozygosity

Heterozygosities were calculated for each locus for each population (Table 2). The *Est3* heterozygosities in the 1987 Necker Island collection were lower than those observed in the Hawaiian Archipelago during 1978–80 as no variants at this locus were observed. However, the 1987 Necker Island average heterozygosity over all loci was 0.023 (assuming monomorphism for the 39 additional loci previously resolved) compared with the value of 0.021 reported in the earlier study. Mean heterozygosities were statistically indistinguishable between the two populations and those observed in the earlier study. It should be noted, though, that differences on the order of 5% heterozygosities may require that large numbers of loci be screened to statistically test significant differences, and tests of heterozygosities are particularly insensitive when comparing low levels of heterozygosity such as observed in this study (Archie 1985).

Discussion

Stability of allele frequencies over at least 7 years was found at *Gpi*, *Mpi*, *Pgm*, *Tpep1*, and *Tpep2*. The gene frequencies of spiny lobster from Maro Reef and Necker Island appear to be stable both between collection sites and between years at all loci, with the exception of the two esterase loci. The variability at

the two esterase loci is of particular concern. Is this variability indeed indicative of genetic isolation between the two sampling localities or of changes in the stock structure?

The data of Shaklee and Samollow (1984) showed that *EstD* allele frequencies fluctuate in spiny lobster. They detected annual significant fluctuations in allele frequency within localities, but these annual fluctuations were parallel among Maro Reef, Necker Island, and an additional locality, Kure Atoll. Thus, the fluctuating frequencies did not lead to any significant differences in allele frequency between localities within years.

Our data, 7 years later, are somewhat consistent with this pattern for *EstD*. We detected significant differences between years, but no significant differences were found between localities sampled the same year. These data support the contention that fluctuations in the northwestern Hawaiian Islands do occur in *EstD* allelic frequencies. The data are insufficient to warrant invoking selection or drift as an explanation; however, one suitable hypothesis might be that these fluctuations were caused by immigration of a closely related population differing only at *EstD* frequencies.

However, unlike the previous data set, our data show a significant difference between the 1987 Necker Island and Maro Reef collections at *Est3*. Such change at a single locus could indicate either selection or stochastic processes operating on the *Est3* allelic frequencies with a lack of gene flow between the two localities.

No significant differences in levels of heterozygosity were detectable. This finding is not surprising. The rate of change in heterozygosity based on random drift is inversely proportional to population size (Hartl and Clark 1989) and is calculated as

$$H_t = (1 - 1/2\,N)^t\, H_0$$

where H_0 is the original heterozygosity value, H_t is the heterozygosity value after t generations, and N is the population size. At most, four generations have passed since the previous sampling. Thus, heterozygosity values should be indistinguishable with population sizes characteristic of a commercially exploitable species.

An analysis of low-frequency or rare alleles is often a more sensitive test to detect changes in variability. We observed a number of low-frequency alleles that were previously detected by Shaklee and Samollow (1984). Gregorius (1980) estimates that a sample size of 754 or greater would be needed to assure a 95% probability of detecting all alleles at a locus with frequencies of 0.01 or greater. Sample sizes were large in the earlier study—ranging from 386 to 666—increasing the probability of detection of rare alleles. Thus, it was expected that some of the previously detected rare alleles would not be observed in the 1987 collections, where sample sizes were 200 or less. Our data suggest that there has been no overall reduction in number of rare alleles within the populations; in fact, we detected rare alleles that were previously undetected.

The unchanged average heterozygosities and the persistence of rare alleles indicate that there has been no measurable loss of genetic variability due to fishing pressure. An additional concern in the management of the lobster fishery is whether each bank is primarily a self-recruiting population with minimal larval recruitment coming from other banks, or whether larval recruitment at any bank comes from an archipelago-wide gyre so the depletion of the spawning stock at any one bank will not affect recruitment to that bank. The significant difference between the 1987 Necker Island and Maro Reef frequencies at *Est3* is consistent with the hypothesis that the banks are largely self-recruiting, although this locus also appears to have varied significantly over time. Additional genetic studies, possibly including more sensitive DNA markers, are warranted to further elucidate the amount of genetic differentiation between these two important lobster populations. At present, though, a conservative management strategy would be based on the existence of two self-recruiting populations rather than a strategy based on a single panmictic unit.

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Abstract.—The impact of oil and gas development on fish populations off Louisiana is presumed significant but poorly understood. This study was undertaken to determine the applicability of a logbook program in developing a long-term database of species composition and relative abundance of fish associated with oil and gas structures. A pilot logbook program involving 120 private vessel owners and 25 charterboat operators was conducted between March 1987 and December 1988. Participants recorded date, fishing time, fishing method, number of anglers, and catch composition at each structure fished. Logbooks from a total of 55 private vessel owners and 10 charterboat operators were used in the analysis. Data collected included 15780 angler hours of fishing effort and 61227 fish caught over the study period. A total of 1719 trips were made to 589 different oil and gas structures with at least 46 different species of fish caught. Red snapper and spotted seatrout were the most commonly caught species and had the highest catch rates. Results differed from past logbook programs and creel surveys, possibly indicating a change in the community of fish associated with oil and gas structures.

A Fishery-dependent Based Study of Fish Species Composition and Associated Catch Rates Around Oil and Gas Structures Off Louisiana*

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Louisiana has long been revered as a "Sportsman's Paradise" and justifiably so, as evidenced by the abundant recreational fishing opportunities. A contributing factor to this "paradise" is the large number of oil and gas platforms acting as defacto artificial reefs. There are approximately 3700 oil and gas structures that constitute 28% of the known hard substrate off Louisiana and Texas (Gallaway 1984). Since the nearest natural hardbottom habitat is approximately 92 km off the Louisiana coast (Sonnier et al. 1976), oil and gas platforms provide the only source of hardbottom habitat (i.e., artificial reefs) close to shore.

Oil and gas platforms are unique as artificial reefs because they extend throughout the entire water column. Due to the size and shape of the structures they are thought to affect benthic, demersal, and pelagic fishes (Gallaway et al. 1981, Continental Shelf Associates 1982). Pelagic baitfish (i.e., round scad *Decaptarus punctatus*, Spanish sardine *Sardinella anchovia*, and scaled sardine *Harengula pensacolae*) often maintain a position from near the surface to mid-depth within or upcurrent from oil and gas structures, while large predatory pelagic fishes (i.e., king mackerel *Scombermorous cavalla*, and blue runner *Caranx crysos*) were reported to swim from the surface to mid-depth around structures (Hastings et al. 1976, Gallaway et al. 1981).

Evidence for the success of platforms as artificial reefs comes from sportfishing which is concentrated around these structures off the coast of Louisiana. An estimated 37% of the total saltwater angling effort and over 70% of all recreational angling trips that venture into the Exclusive Economic Zone (more the 3 miles from shore) off Louisiana occur around platforms (Witzig 1986, Reggio 1987).

In general there is little known about the species associated with oil and gas structures. Reported catch composition of charter boat operators fishing oil and gas platforms included (unranked): snapper (Family Lutjanidae), seatrout *Cynoscion* sp., Atlantic croaker *Micropogonias undulatus*, red drum *Sciaenops ocellatus*, king mackerel, cobia *Rachycentron canadum*, bluefish *Pomatomus saltatrix*, and sharks (Order: Selachii) based on studies by Dugas et al. (1979) and Ditton and Auyong (1984). Similar catch compositions were reported for private vessel anglers (Ditton and Auyong 1984, Stanley and Wilson 1989). In general, bottom fishing was reported to be the predominant fish-

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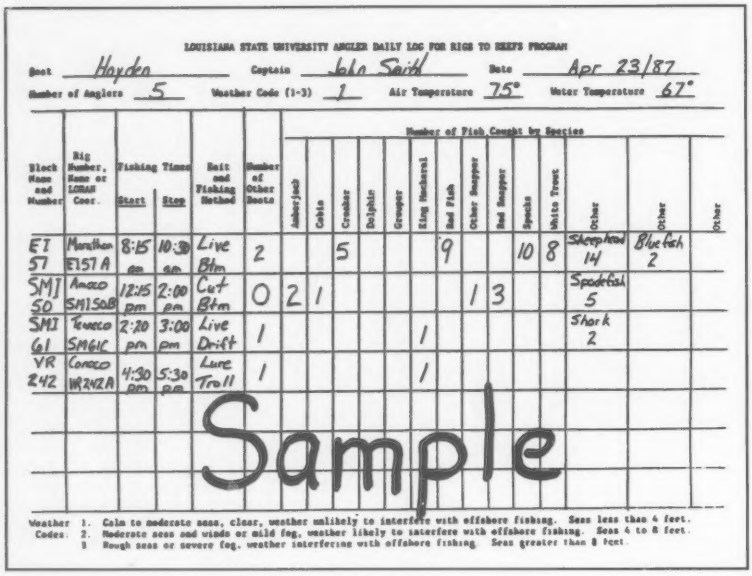
* Contribution No. LSU-CFI-90-01, Louisiana State University, Coastal Fisheries Institute.



LOUISIANA STATE UNIVERSITY ANGLER DAILY LOG FOR RIGS TO REEFS PROGRAM

Boat Hayden Captain John Smith Date Apr 23/87

Number of Anglers 5 Weather Code (1-3) 1 Air Temperature 75° Water Temperature 67°

Block Name and Number	Rig Number, Name or LORAN Coor.	Fishing Times Start	Fishing Times Stop	Bait and Fishing Method	Number of Other Boats	Number of Fish Caught by Species: Amberjack	Cobia	Croaker	Dolphin	Grouper	King Mackerel	Red Fish	Other Snapper	Red Snapper	Speckle	White Trout	Other	Other	Other
EI 57	Marathon E157A	8:15 am	10:30 am	Live Btm	2			5				9			10	8	Sheephead 14	Bluefish 2	
SMI 50	Amoco SMI50B	12:15 pm	2:00 pm	Cut Btm	0	2	1						1	3			Spadefish 5		
SMI 61	Texaco SMI61C	2:20 pm	3:00 pm	Live Drift	1						1						Shark 2		
VR 242	Conoco VR242A	4:30 pm	5:30 pm	Lure Troll	1						1								

Sample

Weather Codes: 1. Calm to moderate seas, clear, weather unlikely to interfere with offshore fishing. Seas less than 4 feet.
2. Moderate seas and winds or mild fog, weather likely to interfere with offshore fishing. Seas 4 to 8 feet.
3 Rough seas or severe fog, weather interferring with offshore fishing. Seas greater than 8 feet.

Figure 1
Sample page from offshore logbook program.

ing method used by charterboat operators and private vessel anglers. However, Dugas et al. (1979) reported that trolling was the dominant fishing method used by private vessel anglers in Louisiana, with bottom fishing second.

Highest catch rates while trolling off the Louisiana coast by charterboat operators from 1982 to 1985, calculated as number of fish caught/boat hour (CPH), were 9.19 for dolphin in 1982 and 9.04 for Spanish mackerel in 1985 (Brusher et al. 1984, Brusher and Palko 1985, 1987). Bottom-fishing catches off the Louisiana coast by charterboat operators consisted chiefly of Atlantic croaker, red snapper, sand seatrout *C. arenarius*, unidentified seatrout, grey triggerfish *Balistes capricus*, bluefish, and king mackerel, with highest CPH's of 23.45 for sand seatrout and 12.38 for Atlantic croaker in 1984 (Brusher et al. 1984; Brusher and Palko 1985, 1987).

A method by which to test the success or value of an artificial reef and develop a data base on species composition is by tracking the number of fish caught over time, under the assumption that catch per unit effort (CPUE) of the target species is proportional to the abundance of fish. The resultant CPUE can then be used as a measure of relative abundance of fish, and the effects of an artificial reef such as an oil or gas platform can be assessed. For the target species of both the avid recreational angler and researcher, CPUE is a good index of relative abundance (Peterman and Steer 1981, Casselman et al. 1985, Richards and Schnute 1986). Users of such data, however, should be aware that the variability of CPUE estimates can be a problem with any sampling program and can change with different sampling gears. However, Casselman et al. (1985) found that the coefficient of variation of angling catches by experienced, avid, or professional fishermen such as charterboat operators was significantly lower than for other sampling techniques such as trawling, electrofishing, gillnetting, and trapnetting.

The goals of this study were to (1) record and quantify the catch rates and species composition for fish caught by recreational anglers and charterboat operators at or near oil and gas platforms off the Louisiana coast; (2) compare our results with past studies from the northern Gulf of Mexico; and (3) determine the utility of using CPUE estimates of the target species caught near the platforms as an index of their relative abundance.

Materials and methods

Volunteers (120) were solicited to maintain log books from fishing clubs across Louisiana. In addition, 23 charterboat operators listed in National Marine Fisheries Service records, and Coleman (1984) volunteered to maintain logbooks. Study participants were provided with logbooks and program information. Monthly contact was made with study participants to ensure their assistance.

Logbook design was based on the Lake Erie Angler Diary Program (Sztramko 1986) and logbook criteria

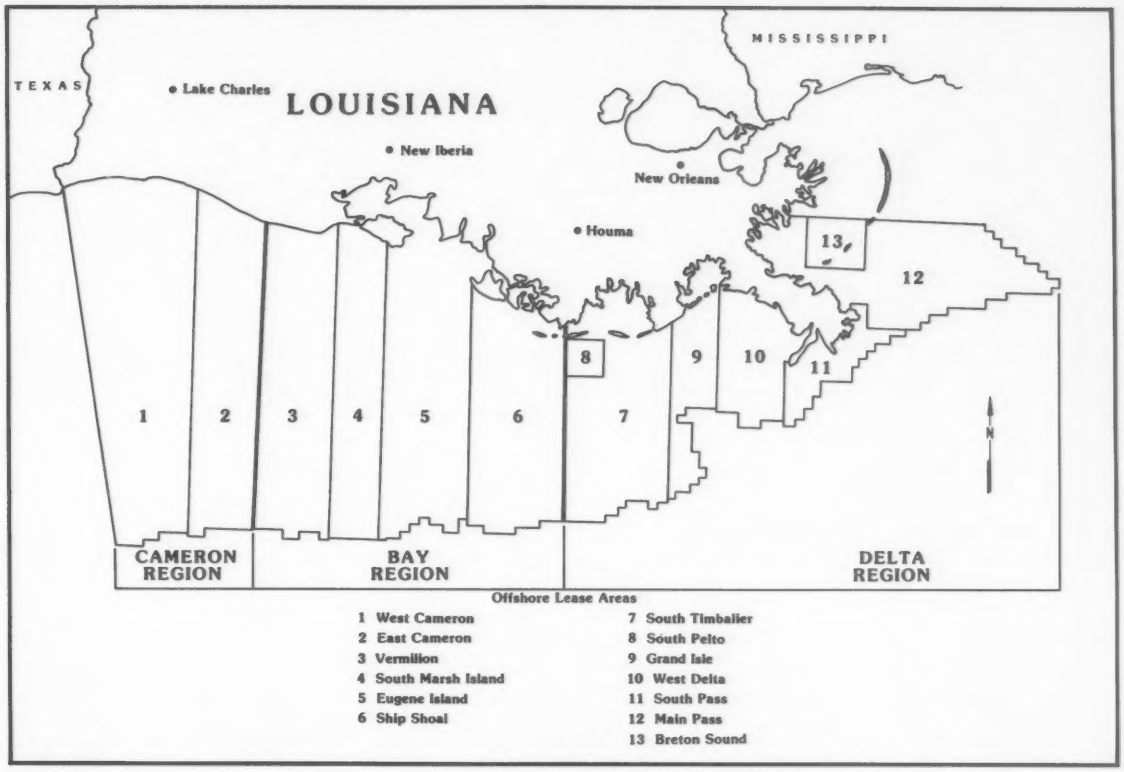


Figure 2
Three regions of the Louisiana offshore study area.

outlined by Demory and Golden (1983). Information entered into the logbooks included date, number of anglers, identity of the oil and gas platform fished, fishing time (not including travel time), fishing method, bait used, and the number of fish caught by species. Participants were asked to complete at least one page of the logbook for each fishing day (Fig. 1). Logbook data were collected from March 1987 to December 1988. Due to the difficulty of identifying certain species of fish such as snapper other than red snapper, groupers, sharks, and silver and sand seatrout, these species were classified as other snapper, groupers, sharks, and silver/sand seatrout, respectively. Other data acquired from study participants included boat length (m), total engine horsepower, and the presence of electronic gear (i.e., LORAN, graph recorders, and echosounders) which aided in the capture of fish. Submerged surface area (m^2) and volume of water enclosed (m^3) by each structure utilized by the participants in 1987 were calculated from schematic diagrams provided by the platform operators.

Fishing effort and CPUE (number of fish caught/angler hour) estimates were separated into two categories: nearshore and offshore fishing. Nearshore fishing around oil and gas platforms was defined as any time at which spotted seatrout were caught, and offshore fishing was defined as trips during which spotted seatrout were not caught. Offshore fishing was further subdivided into bottom fishing (during which time the boat is moored to an oil and gas platform) and trolling. The rationale for the separation of the effort into two categories was due to the segregation of the fish species, as spotted seatrout and red snapper were caught together only 0.7% of the time. Nearshore fishing generally took place in less than 10 m of water where target species were nearshore species such as spotted seatrout, red drum, Spanish mackerel, etc. In contrast, offshore fishing occurred in much deeper water and the target species was usually red snapper; however, a wide range of species were caught with the exception of spotted seatrout. The bait and gear used during the two types of fishing were very different.

Table 1

Descriptive statistics on the number of anglers, man hours, and time spent fishing per oil and gas platform off Louisiana by charterboat operators (CBO) and anglers for inshore fishing and offshore bottom fishing and trolling from logbook records, March 1987–March 1988.

	Time/platform (hrs)				Number of anglers			
	1987		1988		1987		1988	
	Anglers	CBO	Anglers	CBO	Anglers	CBO	Anglers	CBO
Inshore								
N	174	109	62	4	174	109	62	4
Mean	2.8	2.4	2.5	3.6	3.2	3.9	2.8	4.8
SD	2.3	2.3	1.6	2.1	0.8	0.9	0.7	1.0
Offshore bottom								
N	362	578	228	211	362	578	228	211
Mean	2.4	1.3	2.3	1.1	3.7	8.7	3.5	9.6
SD	2.1	1.1	2.1	1.0	2.0	4.6	1.7	3.4
Trolling								
N	130	33	76	14	130	33	76	14
Mean	1.7	2.5	1.4	2.6	3.9	3.5	2.9	4.5
SD	1.8	2.3	1.1	2.3	2.1	1.1	0.9	0.8

While nearshore fishing, light spinning, and bait cast tackle were utilized with natural or artificial baits, offshore fishing tackle generally consisted of heavy boat rods with level wind reels using at least 30-lb test line.

Catch data from various capture methods are usually not distributed normally due to the large number of zero values. Therefore, CPUE was transformed by ln(CPUE + 1) to approximate the normal distribution of the catch data (Pennington 1983, 1985; Shaw et al. 1985). To compare catch rates of red snapper and spotted seatrout between user groups and years, an ANOVA (SAS 1985) was utilized. A Duncan's multiple range test (SAS 1985) was performed to determine differences in red snapper catches between the three regions of coastal Louisiana (Fig. 2). Based on Univariate Analysis (SAS 1985) of the residuals from ANOVA tests and Duncan's multiple range tests, statistical comparisons could only be made between user groups and years for spotted seatrout and red snapper and among areas and years for red snapper to comply with the assumptions of the statistical tests utilized.

Results

A total of 55 private boat operators and 10 charterboat operators returned usable logbooks in 1987, and 30 private boat operators and 5 charterboat operators in 1988, representing return rates of 45.8% and 43.5% in 1987, and 25.0% and 20.8% in 1988, respectively. Participants fished at 589 different oil and gas platforms 1787 separate times over the study period. Anglers fished at oil and gas platforms on 666 occasions in 1987 and 362 times in 1988. Charterboat operators fished at platforms 530 times in 1987 and 229 times in 1988. In 1987, private vessel and charter operator logbook participants spent a total of 2482 hours fishing, representing 11014 angler hours. During 1988, 1057 vessel hours were spent fishing which accounted for 4780 angler hours of fishing. Charterboat operators carried more fishermen than did the private vessels for all three fishing methods (Table 1).

The most prevalent fishing method for both private boat and charterboat anglers during 1987 and 1988 was offshore bottom fishing. Offshore bottom fishing accounted for 54.5% (1987) and 63.2% (1988) of private vessel fishing trips, and 73.2% (1987) and 92.1% (1988) of charterboat fishing trips. Nearshore fishing and trolling were the next most prevalent fishing methods over the survey period (Table 2).

Study participants most often fished at the large multiwell production platforms, based on the mean submerged surface area and volume of water enclosed by a structure, with charterboat operators fishing at larger platforms than private boat anglers for all three types of fishing (Table 3), although the study participants utilized the available size range of structures from single well caissons to semi-submersible drilling platforms.

Table 2
Boat length, engine horsepower, and frequency of presence of electronic equipment for charterboat and angler logbook participant vessels.

	N	Mean	SD	Min.	Max.
Anglers					
Length (m)	55	7.63	2.18	5.18	18.59
Total engine horsepower	55	298.5	183.7	100.0	1200.0
Charterboats					
Length (m)	10	10.09	2.54	7.62	14.33
Total engine horsepower	10	438.5	154.8	225.0	700.0

	Electronic equipment (%)		
	Echosounders	Graph recorders	LORAN
Anglers	72.7	44.5	67.4
Charterboats	68.9	93.8	93.8

Fishing effort was concentrated in late spring, summer, and early fall for both private boat anglers and charter boat operators. The period from May to September in both 1987 and 1988 constituted over 70% private vessel and charterboat fishing trips (Figs. 3, 4).

Participants caught a total of 44465 fish in 1987 and 16792 fish in 1988 from over 46 different species (Table 4). The five most frequently caught species or species groups in 1987 were (in descending order): red snapper, spotted seatrout, silver/sand seatrout, other snapper, and greater amberjack (Table 4). The five most frequently caught species or species groups in 1988 were (in descending order): red snapper, spotted seatrout, other snapper, silver/sand seatrout, and grey triggerfish (Table 4). These five groups represent 73.4% and 70.4% of the total number of fish caught in 1987 and 1988, respectively (Table 4).

CPUE values of spotted seatrout in 1987 were significantly greater ($P<0.01$) than those of 1988 when all data were pooled by user group (Table 5). When the CPUE estimates of each group were pooled by year, CPUE of charterboat operators for spotted seatrout was significantly greater ($P<0.01$) than that of private vessel anglers. Due to the lack of inshore charterboat participants in 1988, comparisons between user groups and years could not be made. The CPUE estimates of spotted seatrout were approximately one order of magnitude greater than those of other commonly caught fish (i.e., bluefish, red drum, and silver/sand seatrout) while inshore fishing during both sample years (Table 5).

Similarly, offshore bottom-fishing CPUE estimates of red snapper during 1987 and 1988 were approximately one order of magnitude greater than those of other commonly caught fish (i.e., Atlantic croaker, bluefish, greater amberjack, grey triggerfish, grouper, other snapper, and silver/sand seatrout) (Table 5).

Table 3
Descriptive statistics on submerged surface area, volume of water enclosed, and water depth of oil and gas platforms fished by logbook participants while trolling and inshore and offshore bottom fishing off Louisiana, 1987. CBO = charterboat operators.

	Submerged surface area (m^2)		Volume of water enclosed (m^3)		Water depth (m)	
	Anglers	CBO	Anglers	CBO	Anglers	CBO
Inshore						
N	149	96	149	96	149	96
Mean	1500.6	3051.8	6878.7	18421.0	7.9	8.8
Min. value	18.7	46.5	18.1	18.1	2.4	3.1
Max. value	13677.8	13677.8	89174.8	89174.8	37.2	62.5
Trolling						
N	122	31	122	31	122	31
Mean	3359.3	11134.0	25915.7	67522.3	26.7	45.4
Min. value	42.0	720.7	0.0	2103.4	6.7	12.2
Max. value	26319.4	144092.6	316654.4	689118.8	129.5	304.8
Offshore bottom fishing						
N	342	361	342	361	342	361
Mean	3705.2	4275.8	27597.7	32673.6	30.1	38.0
Min. value	24.5	151.8	0.0	0.0	3.1	4.0
Max. value	144092.6	144092.6	689118.8	689118.8	304.8	304.8

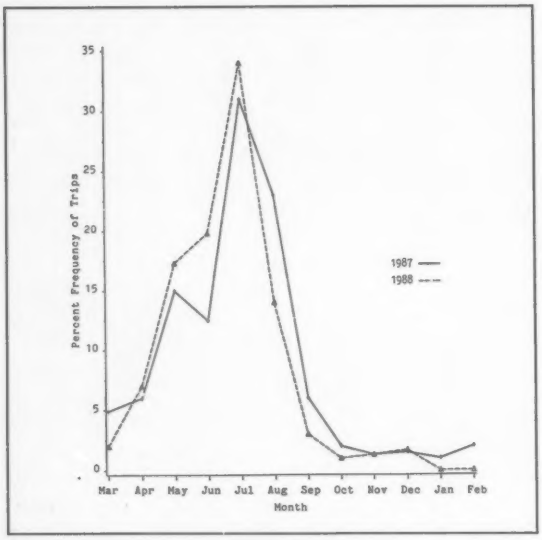


Figure 3
Frequency of offshore fishing trips by month for private vessel angler participants, 1987–88.

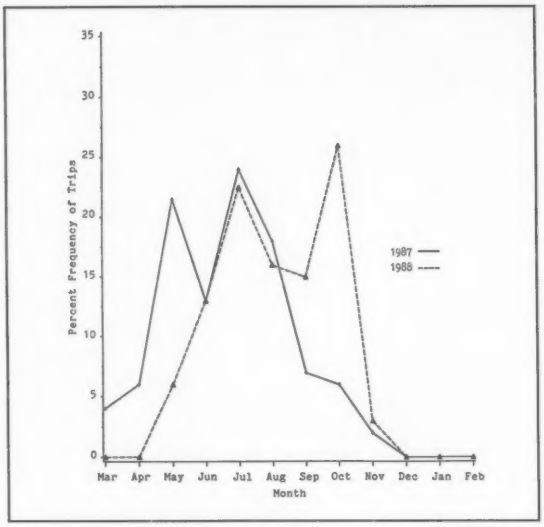


Figure 4
Frequency of offshore fishing trips by month for charterboat operator participants, 1987–88.

Only red snapper were caught often enough to allow statistical comparisons between groups for each year for offshore bottom fishing. Red snapper CPUE of private vessel anglers in 1987 was significantly greater ($P<0.01$) than that of private vessel anglers in 1988 and charterboat operators in 1987 but not significantly greater ($P<0.01$) than that of charterboat operators in 1988.

Offshore trolling CPUE's were not dominated by a single species, nor were they as high as the inshore and offshore bottom fishing CPUE's. Private vessel anglers and charterboat operators most frequently caught blue runner, dolphin, king mackerel, little tunny, and Spanish mackerel while trolling offshore, and the CPUE's of charterboat operators were generally higher, although statistical comparisons were not performed (Table 5).

Private vessel angler and charterboat operator CPUE estimates were pooled for each species to compare CPUE rates between the three regions of coastal Louisiana (Fig. 2) between years. Nearshore CPUE's for all three regions were dominated by spotted seatrout, with the highest CPUE of spotted seatrout found in the Bay region for both 1987 and 1988. The only other striking differences were the CPUE rates of bluefish and red drum which were highest in the Delta region (Table 6). However, due to small sample sizes no statistical comparisons could be performed.

Red snapper CPUE's were the highest in all three regions while offshore bottom fishing. Red snapper CPUE's in the Cameron region during 1987 were significantly greater ($P<0.01$) than those in the Cameron region in 1988; otherwise no significant differences between years or regions for red snapper CPUE were detected (Table 7). Other regional catch differences included much higher CPUE estimates from the Delta region, as opposed to the Cameron and Bay regions, for Atlantic croaker; otherwise no other trends in CPUE were detected between areas or years (Table 7). Due to the large number of zero catches in the species other than red snapper, statistical comparisons could not be performed.

Offshore trolling CPUE estimates from the three regions were not as high or dominated by a single species as were the observed nearshore and offshore bottom-fishing estimates (Table 6). Blue runner, dolphin, little tunny, and Spanish mackerel CPUE's were highest in all three regions. Few trends could be detected between years or regions, as only the CPUE of Spanish mackerel from the Cameron region appeared to be much higher than those of the other species and regions (Table 6), although statistical comparisons could not be made.

Table 4

Composition of catch around oil and gas platforms off Louisiana by logbook participants, 1987–88.

Species/group	1987 No. caught	1987 %	1988 No. caught	1988 %
Atlantic croaker *Micropogonias undulatus*	887	2.0	89	0.5
Atlantic spadefish *Chaetodipterus faber*	23	0.1	110	0.7
Bearded brotula *Brotula barbata*	14	0.0	6	0.0
Black drum *Pogonias cromis*	167	0.4	86	0.5
Blackfin tuna *Thunnus atlanticus*	25	0.1	25	0.1
Bluefish *Pomatomus saltatrix*	1264	2.8	301	1.8
Blue marlin *Makaira nigricans*	4	0.0	1	0.0
Blue runner *Caranx crysos*	279	0.6	256	1.5
Cobia *Rachycentron canadum*	507	1.1	185	1.1
Crevalle jack *Caranx hippos*	63	0.1	26	0.2
Cubbyu *Equetus umbrosus*	5	0.0	—	—
Dolphin *Coryphaena hippurus*	381	0.9	612	3.7
Florida pompano *Trachinotus carolinus*	329	0.7	18	0.1
Flounder *Paralichthys* sp.	8	0.0	12	0.1
Gafftopsail catfish *Bagre marinus*	80	0.2	58	0.3
Great barracuda *Sphyraena barracuda*	93	0.2	19	0.1
Greater amberjack *Seriola dumerili*	1840	4.1	718	4.3
Grey triggerfish *Balistes capriscus*	1221	2.7	990	5.9
Grouper Family: Serranidae	1206	2.7	794	4.7
Grunts *Haemulon* sp.	78	0.2	136	0.8
Hake *Urophycis* sp.	3	0.0	3	0.0
Hardhead catfish *Arius felis*	480	1.1	45	0.3
King mackerel *Scomberomorus cavalla*	543	1.2	201	1.2
Ladyfish *Elops saurus*	29	0.1	3	0.0
Little tunny *Euthynnus alletteratus*	346	0.8	174	1.0
Lookdown *Selene vomer*	9	0.0	28	0.2
Other jacks *Caranx* sp.	54	0.1	9	0.1
Other snapper Family: Lutjanidae	2101	4.7	1355	8.1
Pinfish *Lagodon rhomboides*	127	0.3	74	0.4
Puffer Family: Tetraodontidae	1	0.0	—	—
Rainbow runner *Elagatis bipinnulata*	1	0.0	2	0.0
Rays Family: Dasyatidae	5	0.0	1	0.0
Red drum *Sciaenops ocellatus*	1287	2.9	183	1.1
Red snapper *Lutjanus campechanus*	15385	34.6	6913	41.2
Sharks Order: Selachii	689	1.5	195	1.2
Sheepshead *Archosargus probatocephalus*	39	0.1	25	0.1
Shrimp eel *Ophichthus* sp.	12	0.0	15	0.1
Silver/sand seatrout *Cynoscion* sp.	3663	8.2	974	5.8
Skipjack tuna *Euthynnus pelamis*	624	1.4	258	1.5
Spanish mackerel *Scomberomorus maculatus*	746	1.7	213	1.3
Spotted seatrout *Cynoscion nebulosus*	9688	21.8	1579	9.4
Squirrelfish *Holocentrus* sp.	17	0.0	15	0.1
Tarpon *Megalops atlanticus*	4	0.0	1	0.0
Tripletail *Lobotes surinamensis*	72	0.2	4	0.0
Wahoo *Acanthocybium solanderi*	29	0.1	37	0.2
White spotted soapfish *Rypticus maculatus*	9	0.0	—	—
Yellowfin tuna *Thunnus albacares*	5	0.0	4	0.0
Total	44465		16762	

Table 5

Nearshore, offshore trolling, and offshore bottom fishing CPUE of angler and charterboat operator (CBO) logbook participants, 1987–88, near oil and gas platforms off Louisiana.

	1987				1988			
	Anglers		CBO		Anglers		CBO	
Species/group	Mean	(CV)	Mean	(CV)	Mean	(CV)	Mean	(CV)
Nearshore	$n = 174$		$n = 109$		$n = 64$		$n = 4$	
Bluefish	0.24	(327)	0.03	(491)	0.22	(256)	0.36	(132)
Cobia	0.03	(460)	0.01	(550)	—	—	0.01	(200)
Hardhead catfish	0.03	(593)	—	—	0.05	(526)	—	—
Red drum	0.16	(330)	0.33	(327)	0.18	(189)	0.56	(98)
Sharks	0.04	(509)	—	—	0.02	(445)	—	—
Silver/sand seatrout	0.55	(374)	0.14	(348)	0.63	(288)	1.40	(200)
Spanish mackerel	0.03	(980)	—	—	0.02	(547)	—	—
Spotted seatrout	3.94	(131)	5.48	(74)	3.33	(138)	0.83	(158)
Offshore bottom fishing	$n = 362$		$n = 578$		$n = 222$		$n = 211$	
Atlantic croaker	0.17	(631)	0.08	(330)	0.11	(452)	0.01	(698)
Bluefish	0.30	(510)	0.11	(429)	0.11	(608)	0.01	(549)
Blue runner	0.11	(1129)	0.02	(1061)	0.09	(546)	—	—
Cobia	0.08	(360)	0.06	(323)	0.07	(342)	0.04	(258)
Dolphin	0.05	(916)	0.02	(1207)	0.01	(1051)	0.01	(1087)
Greater amberjack	0.30	(391)	0.25	(272)	0.24	(484)	0.19	(264)
Grey triggerfish	0.28	(311)	0.14	(329)	0.39	(289)	0.19	(160)
Grouper	0.23	(282)	0.22	(255)	0.21	(265)	0.30	(158)
Hardhead catfish	0.11	(641)	0.06	(705)	0.01	(1490)	0.01	(908)
King mackerel	0.04	(364)	0.05	(335)	0.03	(626)	0.04	(299)
Other snapper	0.19	(377)	0.37	(245)	0.05	(321)	0.47	(183)
Red drum	0.11	(385)	0.07	(762)	0.06	(462)	—	—
Red snapper	2.83	(171)	2.11	(155)	2.12	(248)	2.53	(148)
Sharks	0.06	(556)	0.12	(431)	0.04	(608)	0.05	(304)
Silver/sand seatrout	0.82	(388)	0.32	(298)	0.30	(256)	0.01	(693)
Spanish mackerel	0.08	(615)	0.03	(1013)	0.02	(887)	—	—
Offshore trolling	$n = 130$		$n = 33$		$n = 76$		$n = 14$	
Blue runner	0.34	(308)	0.03	(441)	1.02	(229)	0.03	(374)
Cobia	0.02	(397)	0.08	(266)	0.01	(699)	0.02	(296)
Crevalle jack	0.07	(398)	0.10	(446)	0.05	(387)	—	—
Dolphin	0.26	(372)	0.71	(236)	0.25	(502)	1.23	(167)
Greater amberjack	0.12	(598)	0.09	(377)	0.09	(356)	—	—
King mackerel	0.11	(623)	0.62	(151)	0.25	(232)	0.17	(171)
Little tunny	0.43	(222)	0.85	(209)	0.78	(162)	0.21	(241)
Other jacks	0.07	(623)	0.08	(400)	0.02	(872)	—	—
Spanish mackerel	0.51	(271)	0.64	(222)	0.84	(227)	0.42	(288)

Discussion

Private vessel anglers and charterboat operators caught a total of 61227 fish representing over 46 different species. The fishing habits and boat characteristics of study participants were as expected. Peak fishing by private vessel anglers and charterboat operators occurred during the summer which agreed with past studies by Ditton and Auyong (1984) and Stanley and Wilson (1989). During other times of the year, cold fronts and other severe forms of weather make fishing off the coast of Louisiana nearly impossible or at least uncomfortable. Based on number of trips, the most prevalent fishing method was offshore bottom fishing, with nearshore and offshore trolling the next most popular methods for the study participants.

Private vessel anglers and charterboat operators utilized the entire range of platform sizes and operational types off the coast of Louisiana. Single well structures, steel template platforms, and mobile semisubmersible drilling platforms were commonly fished, although certain trends in platform size utilization and fishing method were apparent. Nearshore anglers most often fished at the small, single well structures

Table 6

Nearshore and offshore trolling CPUE of logbook participants around oil and gas platforms in the Delta, Bay, and Cameron Regions off Louisiana, 1987–88.

	Delta		Bay		Cameron	
	1987	1988	1987	1988	1987	1988
Species/group	Mean (CV)	Mean (CV)	Mean (CV)	Mean (CV)	Mean (CV)	Mean (CV)
Nearshore	$n = 48$	$n = 8$	$n = 196$	$n = 46$	$n = 37$	$n = 12$
Bluefish	0.68 (197)	1.28 (64)	0.04 (537)	0.02 (678)	0.14 (324)	0.22 (234)
Cobia	0.06 (259)	0.03 (144)	0.01 (947)	— —	0.02 (370)	— —
Hardhead catfish	— —	— —	0.03 (606)	0.07 (444)	— —	— —
Red drum	0.99 (169)	0.80 (49)	0.02 (660)	0.11 (249)	0.39 (258)	0.07 (186)
Sharks	0.01 (495)	0.03 (494)	0.03 (632)	0.03 (439)	0.05 498)	— —
Silver/sand seatrout	0.25 (326)	0.08 (282)	0.38 (444)	0.85 (249)	0.53 (226)	0.55 (293)
Spanish mackerel	0.09 (557)	— —	0.02 (608)	0.01 (475)	0.02 (608)	0.07 (346)
Spotted seatrout	1.73 (125)	0.48 (70)	5.70 (87)	4.28 (119)	2.02 (97)	1.29 (83)
Offshore trolling	$n = 78$	$n = 50$	$n = 23$	$n = 13$	$n = 63$	$n = 27$
Bluerunner	0.46 (260)	0.71 (230)	0.20 (425)	1.06 (234)	0.09 (441)	1.06 (269)
Cobia	0.04 (372)	0.02 (592)	0.03 (303)	— —	0.03 (369)	0.01 (388)
Crevalle jack	0.01 (590)	— —	0.07 (268)	0.07 (361)	0.15 (311)	0.10 (263)
Dolphin	0.20 (276)	0.48 (363)	0.68 (298)	0.15 (177)	0.40 (312)	0.39 (298)
Greater amberjack	0.05 (630)	— —	0.14 (315)	0.27 (158)	0.18 (509)	0.12 (350)
King mackerel	0.04 (455)	0.05 (506)	0.07 (209)	0.29 (165)	0.49 (157)	0.55 (140)
Little tunny	0.69 (205)	0.73 (173)	0.14 (215)	0.50 (174)	0.43 (199)	0.72 (174)
Other jacks	0.08 (625)	0.03 (707)	0.14 (381)	— —	0.05 (498)	— —
Spanish mackerel	0.25 (363)	0.24 (262)	0.28 (270)	0.46 (302)	1.06 (196)	1.91 (145)

Table 7

Offshore bottom fishing CPUE of logbook participants around oil and gas platforms in the Delta, Bay, and Cameron Regions off Louisiana, 1987–88.

	Delta		Bay		Cameron	
	1987	1988	1987	1988	1987	1988
Species/group	Mean (CV)	Mean (CV)	Mean (CV)	Mean (CV)	Mean (CV)	Mean (CV)
	$n = 627$	$n = 280$	$n = 196$	$n = 77$	$n = 153$	$n = 75$
Atlantic croaker	0.16 (518)	0.10 (485)	0.02 (694)	— —	0.04 (393)	— —
Bluefish	0.23 (592)	0.02 (539)	0.11 (422)	0.25 (437)	0.08 (689)	0.02 (672)
Cobia	0.05 (367)	0.05 (362)	0.14 (310)	0.08 (282)	0.08 (242)	0.05 (273)
Greater amberjack	0.30 (331)	0.11 (487)	0.18 (325)	0.15 (235)	0.25 (224)	0.65 (275)
Grey triggerfish	0.26 (287)	0.25 (217)	0.07 (571)	0.50 (288)	0.09 (386)	0.23 (391)
Grouper	0.26 (238)	0.30 (183)	0.16 (416)	0.20 (283)	0.15 (277)	0.15 (230)
King mackerel	0.02 (449)	0.03 (384)	0.07 (198)	0.02 (330)	0.14 (224)	0.07 (439)
Other snapper	0.40 (240)	0.56 (217)	0.13 (508)	0.55 (329)	0.07 (336)	0.14 (542)
Red drum	0.10 (524)	0.02 (876)	0.09 (633)	0.02 (445)	0.05 (338)	0.08 (356)
Red snapper*	2.33 (187)[ab]	2.27 (162)[ab]	2.62 (124)[ab]	2.72 (247)[ab]	2.85 (132)[a]	2.19 (237)[b]
Sharks	0.11 (421)	0.05 (428)	0.03 (379)	0.04 (591)	0.08 (596)	0.02 (301)
Silver/sand seatrout	0.68 (369)	0.20 (328)	0.17 (383)	0.15 (363)	0.12 (460)	0.02 (699)
Spanish mackerel	0.02 (1153)	0.01 (1471)	0.12 (536)	0.01 (560)	0.12 (498)	0.02 (442)

*Means with the same letter are not significantly different at the 1% level.

in shallow water, while offshore bottom fishing and trolling anglers fished much larger steel template platforms in deep water. These results provide evidence that participants were maximizing their catch potential, as Stanley (1989) found highest abundances of spotted seatrout near small platforms in shallow water, while highest abundances of red snapper and related species were found near large platforms (sub-

merged surface area 8000–14000 m^2) in 70–100 m of water.

Charterboat operators had larger vessels than private vessel anglers due to the business nature of their fishing and larger party size. Using larger vessels, they were able to fish in deeper waters farther offshore than private vessel anglers for both offshore bottom fishing and trolling. Charterboat operators also fished in deeper water while fishing nearshore; however, this is probably not a direct function of boat size, but of past success and preference.

A high diversity of fish exist around the oil and gas platforms as evidenced by the reported catch of over 46 different species. The types of fish caught ranged from relatively common and highly desirable species such as spotted seatrout, red snapper, tarpon, blue marlin, king mackerel, and yellowfin tuna to rather rare fishes such as hake, bearded brotula, and squirrel fish. However, catches by angling are selective and biased towards larger, carnivorous individuals due to the gear utilized (Grimes et al. 1982). Therefore, species not susceptible to angling were not represented.

Comparison of CPUE estimates between this study and logbook programs from other parts of North America revealed CPUE estimates were generally much higher off the Louisiana coast than from other studies. CPUE estimates from Sztramko (1986) for Lake Erie, Ontario, private vessel anglers and charterboat operators were approximately 0.15 for the target species of smallmouth bass *Micropterus dolomieui* and coho salmon *Oncorhynchus kisutch*, while Casselman et al. (1985) reported CPUE estimates of 0.30 for northern pike *Esox lucius* by sportfishing guides on the St. Lawrence River, Ontario. Only CPUE estimates from logbooks maintained by commercial fishermen trolling for Pacific salmon (Jordan and Carter 1987) were as high as CPUE estimates from this study.

Catch rates in this study, presented as number of fish per angler per hour, are not directly or statistically comparable with those reported by Brusher et al. (1984), Brusher and Palko (1985, 1987), and other earlier studies from the Gulf of Mexico because they used number of fish caught per boat per hour (CPH) as a unit of relative abundance. Since the number of anglers on a sportfishing vessel can be highly variable, catch per vessel hour may also be highly variable. By calculating the number of fish caught per angler hour, catch is broken down to its most standard unit, assuming the skill level of anglers is equal, thus eliminating this source of variance.

CPH rates by bottom fishing and trolling from this and other studies off the Louisiana coast were much higher than in other regions of the Gulf of Mexico and the southeast Atlantic. However, when mean number of anglers was multiplied by CPUE for charterboat operators from this study and compared with Brusher et al. (1984) and Brusher and Palko (1985, 1987), similar catch rates were noted for the Louisiana coast.

Comparison of the catch rates and composition of trolling from this study and others revealed few differences. Brusher et al. (1984) and Brusher and Palko (1987) found trolling catches of charterboat operators off Louisiana were primarily comprised of dolphin, Spanish mackerel, red drum, little tunny, king mackerel, and blue runner. We found little change in this trend with the exception of red drum. Based on our results, red drum do not appear to be associated with oil and gas structures. Other logbook programs off the Louisiana coast did not distinguish between areas fished (near oil and gas platforms or otherwise) (Dugas et al. 1979), and consequently red drum catches may have been high in areas not covered by our logbook program, which may explain their absence from our results.

When catch rates and composition of our study were compared with those of other logbook programs and a creel census for offshore bottom fishing, major differences in catch composition were noted. Past studies conducted during 1978 by Dugas et al. (1979), in 1982 by Brusher et al. (1984), and during 1984–85 by Brusher and Palko (1987), found that Atlantic croaker and silver/sand seatrout dominated catches of charterboat operators while we found that red snapper catch rates were often an order of magnitude greater than for all other species caught. Since many of the same charterboat operators were utilized by both ours and earlier studies, these differences may provide evidence that there has been a shift in the species abundance near oil and gas platforms in offshore waters with little or no change in the composition of the structure (i.e., the number of oil and gas platforms) off the Louisiana coast. Comparison of our nearshore catches around oil and gas platforms with those of creel surveys of Texas bay charterboat operators from 1978 to 1979 (McEachron and Matlock 1983) showed that spotted seatrout dominated the catch rate and composition of nearshore Texas fishermen as they did in Louisiana, although spotted seatrout catches off Louisiana were much higher than for Texas sport fishermen.

Overall CPUE's of all species between private vessel anglers and charterboat operators were very similar; however, charterboat operator CPUE was generally less variable. Few trends were identified from comparisons between years or user groups. Only for spotted seatrout was charterboat operator CPUE consistently higher than private vessel angler CPUE; otherwise few differences were noted between the two groups. The similarity of the CPUE's indicated that the anglers participating in the logbook program were avid,

knowledgeable fishermen who were as skilled as the professional charterboat operators.

The CPUE of the study participants was probably much higher than that for average offshore saltwater fishermen in Louisiana. Since charterboat operators are professional fishermen who make their living by catching fish, and the private vessel anglers participating in the program were equally as skilled, the catch rates by these groups do not reflect average catches. Both groups have a higher success rate than do casual fishermen who rarely catch fish due to improper techniques and do not target their effort (Casselman et al. 1985). Consequently, the CPUE's presented are not applicable to all fishermen, only to skilled, dedicated, amateur anglers and charterboat operators.

Spotted seatrout and red snapper were the target species of private vessel anglers and charterboat operators, as indicated by their domination of respective CPUE estimates for nearshore and offshore bottom fishing and based on past research from a saltwater recreational angling survey (Stanley and Wilson 1989). Casselman et al. (1985) reported that the CPUE of avid recreational fishermen can be used as an index of relative abundance, and if data are collected over a long period of time, changes in CPUE can reflect fluctuations in the populations of the target species. Offshore trolling CPUE was not dominated by a single species, indicating that fishermen were not targeting their effort for any particular species; therefore, CPUE estimates while trolling would not reflect changes in abundance to the same extent as nearshore and offshore bottom-fishing CPUE estimates.

Conclusions

The catch rates of private vessel anglers and charterboat operators around oil and gas platforms in the northern Gulf of Mexico were high, with their effort targeted towards red snapper while offshore bottom fishing, and spotted seatrout while nearshore fishing. Catch rates while trolling were more uniform and not dominated by any one species. Catch rates between the user groups and across the regions were similar, although some minor differences were detected.

Based on comparisons of catch rates and composition between our results and past studies, a shift in the abundance of certain species has occurred near oil and gas platforms off the Louisiana coast. Studies from 1978 to 1985 found Atlantic croaker and silver/sand seatrout constituted the largest portion of the catch and had the highest catch rates, while we found that red snapper dominated the catch statistics while offshore bottom fishing. Little change in the patterns of species abundance appears to have occurred for species targeted while offshore trolling and nearshore fishing around oil and gas platforms, based on comparisons with earlier studies.

The physical construction of oil and gas platforms precludes the sampling of the associated sportfish populations using traditional methods (e.g., gillnets, trawls). The success of this logbook program indicates that the collection of CPUE data over long periods of time may be an effective technique of monitoring fish populations associated with the platforms. Although the data supplied by the logbooks is an index of relative abundance of fish susceptible to angling and is biased towards larger individuals, it provides a valuable source of data which is otherwise difficult to obtain.

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Abstract.—King crabs *Paralithodes camtschaticus* and Tanner crabs *Chionoecetes bairdi* captured incidentally by Bering Sea trawlers were examined for immediate mortality, vitality, and injuries resulting from trawl capture. A number were held aboard ship for 2 days in seawater to determine delayed mortality. Overall survival, including immediate and delayed effects, was 21% (±2.0%) for king crabs and 22% (±3.6%) for Tanner crabs. Immediate mortality of king crabs decreased significantly with shell age, and increased significantly with time in captivity prior to assessment, from 0% at 3 hours to 100% at 17 hours. Vitality, an index of spontaneous activity level, was a better predictor of delayed mortality than was the presence/absence of injuries. The effect of leg and body injuries on mortality of king crabs was similar, but injuries to leg segments proximal to the plane of autotomy resulted in higher mortality than injuries distal to the autotomy plane, or autotomization alone.

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Survival of King and Tanner Crabs Captured by Commercial Sole Trawls

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Capture and subsequent mortality of nontarget (bycatch) species is a major problem facing managers of multispecies fisheries. In the U.S. eastern Bering Sea (EBS), joint-venture (JV) trawl fisheries targeting on yellowfin sole *Limanda aspera*, rock sole *Lepidopsetta bilineata*, and Pacific cod *Gadus macrocephalus*, routinely catch red king crabs *Paralithodes camtschaticus* and Tanner crabs *Chionoecetes bairdi* and *C. opilio*. In 1988, 88000 red king crabs, 751000 *C. bairdi*, and 2.4 million *C. opilio* were captured in 1.30 million metric tons (t) of groundfish by JV fishing vessels, representing catch rates of 0.07, 0.58, and 1.84 crabs/t, respectively (Berger and Weikart 1989). Additional quantities of these crab species were also captured by domestic fishermen, but their numbers are unknown due to the absence of an effective domestic fishery observer program. All three species of crab are designated as 'Prohibited species' by the North Pacific Fishery Management Council (NPFMC), and must be returned to sea. Nonetheless, mortality of incidentally caught crab is considered to be 100%, and represents losses from the directed crab fisheries.

Due to concerns expressed by crab fishermen about the effects of bycatch on crab populations, a portion of the EBS was closed to trawling by the NPFMC in 1986 to protect king crabs, and has remained closed to date. In addition, maximum catch rates (crabs/t) and caps on total crab catch have been defined for particular regions of the EBS. Somerton and June (1984) attempted to quantify the relative costs to the crab fishery and benefits to the trawl fishery from conducting trawl fisheries on crab grounds, in order to designate those areas with negative relative costs as a king crab conservation zone, but their recommendations were never implemented per se.

The establishment of caps and maximum allowable catch rates was predicated on the assumption that all crabs captured incidentally to trawl fisheries subsequently die. However, this is not necessarily the case. In August of 1988, the opportunity arose to conduct an experiment to determine the survival rate of crab caught incidentally by the JV trawl fishery. This was conducted in conjunction with a study to determine the effectiveness of experimental nets designed to reduce the bycatch of crab. The goals of the study were to determine immediate and delayed survival and mortality of crabs, and the effects on survival of injuries, size and shell age of crabs, processing time, and gear (trawl) type.

Materials and methods

Definitions

The term survival (S), as used in this report, means the proportion of a given group of crabs which was alive at a specified time. Mortality (M) is the complement of this value, i.e., 1 – S. In this investigation, survival was treated as a two-step process; immediate survival (ISURV) or mortality (IMORT) is the proportion determined to be alive or dead, respectively, when the crabs were first

examined and measured. Delayed survival (DSURV) or mortality (DMORT) is that portion alive or dead after crabs were held in seawater for a specified time period.

Sampling technique

An experiment was conducted during the period 12 August–12 September 1987 to compare catch rates between standard Bering Sea joint venture commercial sole trawls and two experimental nets designed to reduce the bycatch of crabs (Highliners Association 1988). Although the results of that experiment are not discussed in this report, the experimental design will be briefly described in order to facilitate understanding of the survival experiment. During the study, five Bering Sea combination trawlers made 307 tows within an area of the EBS between lat. 57° and 58°N, and between long. 162° and 163°W. Tows ranged from 1 to 6.4 hours in length and averaged 20 metric tons (t) of fish. Target species were yellowfin sole *Limanda aspera*, rock sole *Lepidopsetta bilineata*, and Pacific cod *Gadus macrocephalus*. One vessel fished continuously with a previously used 'Standard' trawl (STD). The four other vessels rotated four trawls between them including two new and unused standard trawls, referred to as 'Control 1' (C1) and 'Control 2' (C2), and two experimental trawls. One of the experimental trawls, referred to as the 'Panel' (PAN) trawl, had the front portion of the bottom panel removed and replaced with longitudinal lines, such that crabs could fall out the bottom of the net after passing over the footrope. The second experimental trawl, referred to as the 'Chute' (CHU) trawl, had a webbed funnel-shaped chute sewn into the lower half of the net at the junction between the belly and intermediate section, such that anything entering the mouth of the chute would exit the bottom of the net. During the experiment, codends from each trawl were delivered to the USSR MV *Sulak* at 2–3 hour intervals, where they were sampled by biologists before processing.

Once onboard the *Sulak*, codends were dumped, and all crabs were recovered by sorting through the entire catch. The first 21 tows were dumped on deck and crabs sorted there. The remainder of the tows were dumped directly into storage bunkers, and crabs were recovered from the processing line conveyor in the factory, as the fish were processed. All crabs were sorted by species (and usually by sex), placed into plastic baskets (~25 kg capacity), and weighed. Because of logistic constraints, higher priority was assigned to collecting data on king crabs than on Tanner crabs. Total numbers were determined either by direct counting, or by counting and weighing a subsample. When subsampling occurred, each crab was assigned a sampling factor equal to the proportion of the total number of crabs in the tow represented by the subsample. Crabs were then treated in one of four ways:

(A) Measured crabs Up to 150–200 crabs of each species from each haul were measured to the nearest 1.0 mm with steel vernier calipers. Subsampling occurred when >200 of either species were captured. King crabs were measured from the rear of the right eyesocket to the midpoint of the rear margin of the carapace (carapace length, CL). Tanner crabs were measured across the widest portion of the carapace, including spines (carapace width, CW). Shell conditions were coded as 1 = molting, or recently molted with a soft or flexible shell; 2 = hard shelled but molted within recent year, without epifauna or scratches; 3 = oldshell or skipmolt, with scratches, epifauna, scars, or damaged dactyls.

(B) Vitality coding For most hauls, all measured crabs were also given a vitality code on a 3-point scale: (1) alive and active, i.e., exhibiting spontaneous vigorous movement of appendages and attempting to escape or pinch the examiner; (2) moribund (alive but inactive), i.e., exhibiting only slow weak movements, or only in response to prodding; and (3) dead. In practice, death was not easy to determine, as some crabs which initially appeared dead would exhibit spontaneous movements after examination. After the first few tows, a criterion was developed which consisted of (a) looking for spontaneous movement of appendages, (b) lacking that, attempting to stimulate movement by moving and bending appendages, followed by (c) flicking the mouthparts with a finger three times at 5–10 second intervals. The minimum requirement for a vitality code of 2 was any spontaneous movement of the antennules or any other appendage. These criteria were tested by placing 30 crabs which were classified as dead into the live tanks; none recovered. Presence or absence of injuries was not a criterion used in this coding procedure.

(C) Injury assessment Approximately 30–40 king crabs per tow (usually the first basket examined of each sex) and occasional Tanner crab were examined for injuries. Since there was considerable shuffling and repositioning of crabs and baskets during the weighing and subsampling process, this was assumed to be a random sample, and represents a subset of the crabs examined for vitality in step B above. Examination entailed a visual scan of the carapace, sternum, abdomen, and each leg in turn. Bodily injuries were recorded as present or absent. Leg injuries were categorized as being distal to the autotomy or breakage plane, proximal to the breakage plane, or recent autotomy, distinguished by the presence of a clear membrane with

no discoloration or scarring. The number of legs with each of these three types of injuries was recorded.

(D) Survival or delayed mortality A subset of the injury-assessed crabs (Step C) was placed into one of four tanks of flowing seawater, ~1.0 × 1.0 × 0.7 m, and held for 48 hours, after which they were reexamined for delayed mortality, using the same procedures outlined above for vitality. The subset usually consisted of all crabs coded for injures from one haul per day, although towards the end of the experiment several hauls per day were treated in this manner. Crabs which were determined to be dead before placement into the tanks were retained for at least 6 hours for confirmation before removal.

Crab processing time was recorded for each tow as the interval between the arrival of the codend on deck and the time the crabs were examined and measured. Although examination usually required anywhere from 0.5 to 1.5 hours for an entire sample, the midpoint of that period was used as the mean endpoint of processing time for all crabs in a haul. Towing time, i.e., the difference between the time the net was determined to be on bottom and the time haulback started, was obtained from each catcher vessel and divided by 2, in order to approximate the average time each crab spent in the net before delivery to the *Sulak*. Total capturing and processing time (CAPTIME) was calculated as the sum of (towing time)/2 and processing time.

Total weight of the catch in each haul was estimated by measuring the height and width of the codend at several intervals along its length, and calculating the volume based on the shape of an oblate cylinder, with density determined by weighing a known volume of fish.

Data analysis

In order to improve the precision of the survival estimates, overall survival was calculated for each species in a stratified manner (Cochran 1963). Vitality codes were used as strata because they provided additional information on the probability of survival, i.e., crabs coded as alive and active were deemed more likely to survive than crabs coded as moribund. For immediate survival estimates only, each crab was weighted by the sampling factor for the tow from which it originated. Estimates of delayed mortality were not weighted, because subsampling was accounted for at the level of immediate mortality. The formulae used were:

$$S_{st} = 1/N \sum N_v p_v \quad (1)$$

and

$$V(S_{st}) = 1/N^2 \sum N_v(N_v - n_v)p_v q_v/(n_v - 1) \quad (2)$$

where S_{st} = stratified estimate of population survival rate,
$V(S_{st})$ = variance of stratified estimate,
N_v = number of crabs in stratum (vitality group) v,
n_v = number sampled from stratum v (placed in live tanks),
p_v = proportion of subsample surviving in live tanks,
$q_v = 1 - p_v$,
N = weighted total number of crabs given vitality codes.

The effect of CAPTIME on immediate mortality was determined by fitting the data to a logistic curve. Crabs were grouped into hourly intervals of CAPTIME (as described above), and mortality data (weighted by sampling factors) for each interval were fitted using an iterative procedure (FSAS FISHPARM, Saila et al. 1988). The equation fitted was:

$$M = 1/\{1 + \exp(-r[X - X_{50}])\} \quad (3)$$

where M is expected mortality and $0 \leq M \leq 1$, X is the value of the predictor variable (CAPTIME) in hours, and r and X_{50} are parameters of the equation, the latter representing the time required for 50% mortality to occur. Both king and Tanner crabs were treated separately. Delayed and overall survival were not fitted because there were too few observations. The effect of total catch weight on immediate survival was also determined in the same manner, with crab data grouped by catch weight intervals of 1.0 t.

To determine the effect of size, crabs were grouped by 15-mm intervals of CL (king crab) or CW (Tanner crab). For king crabs, immediate, delayed, and overall mortality were calculated for each size group. Only immediate mortality was calculated for each size group of Tanner crabs, due to limited data. Immediate mortality was also determined for each gear type, by species.

Procedures used by National Marine Fisheries Service (NMFS) observers aboard fishing vessels to code crab vitality differ from those used in this study. In this study, vitality codes were based on activity level of crabs regardless of injuries, and injuries were coded separately, whereas the NMFS observer method is to assign a vitality code of 1 for crabs which are active and uninjured, and a vitality code of 2 for crabs which are either inactive or injured. Contingency table and loglinear analysis was performed in order to assess the difference between these two methods and determine which provided the best estimate of delayed mortality, and to determine the relative contribution of vitality and injuries to subsequent delayed mortality. Three

sets of 2×2 contingency tables were analyzed using the X^2 statistic, which is approximately distributed as the chi-squared distribution, and which is equivalent to the G-statistic for 2×2 contingency tables (Sokal and Rohlf 1981). Only two-way interactions can be identified with this procedure, so factors tested were vitality vs. injuries, vitality vs. mortality, and injuries vs. mortality. The null hypothesis tested was that effects of both factors were independent of each other, i.e., that no interactions occurred.

Loglinear analysis was accomplished to determine the odds of mortality associated with vitality level and injury presence. The SPSS LOGLINEAR (SPSS Inc. 1986) procedure was used to fit a logit model, in which one dichotomous factor—delayed mortality (DMORT)—was designated as a dependent variable, and the remaining factors—vitality (VIT) and injuries (INJ)—were the independent variables. Only live crabs were used, i.e., those with vitality codes of 1 or 2; injury codes were 1 (uninjured) or 2 (injured), and DMORT was coded as 1 (survived) or 2 (died). The data fit by the model were the log-transformed survival odds (ratio of survivors to mortalities), often referred to as logits, in each category of the independent variables (vitality and injuries):

$$\text{Logits} = \ln(\text{ODDS}) = \ln(f_s/f_m) \quad (4)$$

where f_s and f_m are the observed frequencies of survivors and mortalities, respectively. The logit model used for fitting entails expressing the logits as a linear model of several parameters:

$$\ln(f_s/f_m) = 2(l_D + l_{D*V} + l_{D*I}) \quad (5)$$

where f_s, f_m = observed number of survivors or mortalities,
l_D = parameter estimate for DMORT (mean odds of mortality),
l_{D*V} = parameter for interaction of DMORT and vitality,
l_{D*I} = parameter for interaction of DMORT and injuries.

The proportion of crabs in any cell of the model which survive is related to the survival odds by the formula:

$$S = (1 + \text{ODDS}^{-1})^{-1} \quad (6)$$

This model assumes that a mean level of mortality would occur regardless of other factors, and that each confounding factor increases mortality in a logarithmic fashion, or that the overall odds of survival are the sum of the logs of the parameter estimates for each contributing factor. In this model, there are two alternative outcomes for each category, which have equal and opposite parameter values which must sum to 0. For instance, parameter 1 represents the alternatives of survival vs. mortality; parameter 2 represents the positive contribution of a 'good' vitality code of 1 vs. the negative influence of a 'poor' vitality code of 2; parameter 3 is similar to parameter 2 with regard to the influence of the presence vs. absence of injuries. Since the model represents the log of a ratio, the effect attributable to any single factor is calculated as the difference between parameter estimates for alternative outcomes, e.g., the total effect of DMORT is $l_D - (-l_D)$, or $2(l_D)$. Thus the entire equation is multiplied by a factor of 2.

Table 1
Number of crabs sampled during survival study. Each category below "Measured" is a subset of the one above it.

Disposition	King crab	Tanner crab
Measured	18804	31318
Vitality coded	6113	4645
Injuries coded	2835	518
Survival coded	617	74

Each cell of the contingency table was coded as 1 or 2 for each factor. Crabs which were active, uninjured, and survived, for instance, were coded as 1,1,1. Similarly, crabs which were inactive, injured, and died were coded 2,2,2. The parameter value for the effect of vitality on mortality (l_{D*V} in the above model) was calculated for cases with equal codes for DMORT and VIT (i.e., both equal to 1 or both equal to 2); the parameter estimate for cases with unequal codes was equal but opposite in sign. Individual parameters were converted to odds by calculating the antilog. Odds for any combination of categories is equivalent to the product of antilogs of parameters (or the sum of all parameters times 2) for all factors in the model.

The interaction of immediate mortality (IMORT) with body injuries (BODY) and leg injuries (LEGS) was investigated in an identical manner. Values of the variables BODY and LEGS were set to 1 if no injury was present, or 2 if an injury was present.

Contingency table analysis using the X^2 statistic was performed to test the null hypothesis that immediate mortality was independent of three types of leg injury, defined as autotomization, injuries distal to the autotomy or breakage plane, and injuries proximal to the breakage plane. The X^2 statistic was also used to test the independence of immediate and delayed mortality from shell condition, and the number of legs with injuries.

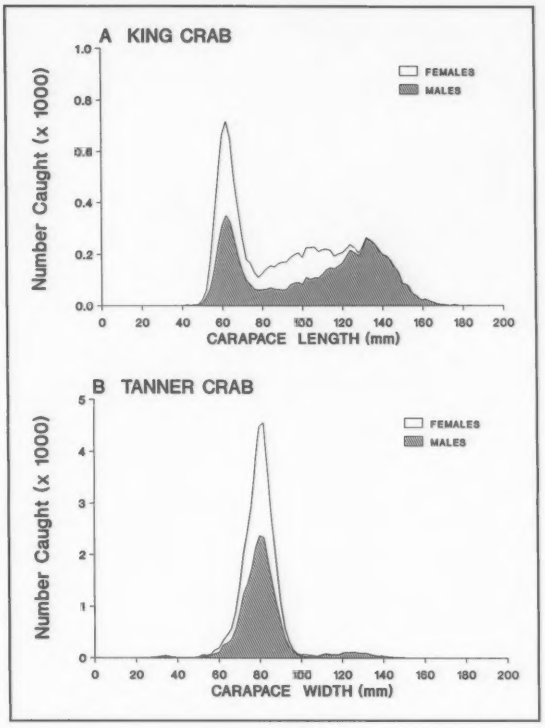

Figure 1
Size frequency of crabs caught during the experiment, shown as a moving average of three 1-mm intervals. Numbers are expanded from number measured by sampling factors. Sexes are stacked.

Results

Over 6200 t of fish were sorted through during the study, and over 50000 crabs were recovered and measured (Table 1), the majority being Tanner crabs (which shall be used herein to refer only to the species *Chionoecetes bairdi*), and the remainder mostly king crabs *Paralithodes camtschaticus*. A few *C. opilio* were encountered but are not discussed here. Vitality was coded on over 10750 crabs, representing 23985 total crabs after expansion by subsampling factors. Injuries were recorded for 3353, and 691 were held in tanks for delayed mortality studies. The size distribution of king crabs was bimodal (Fig. 1A); males exhibited modes near 62 and 135 mm CL, and females near 62 and 100 mm CL. Both sexes of Tanner crabs exhibited a single mode near 80 mm CW (Fig. 1B).

Overall survival

Overall survival was 21% (± 2.0%) for king crabs, and 22% (± 3.6%) for Tanner crabs (Table 2). Results for Tanner crabs are less accurate because fewer crabs were retained, especially from vitality group 1. Virtually no crabs were recorded as moribund after holding in live-tanks, regardless of initial condition; crabs either "recovered" or died. Potential sublethal effects, such as reduced feeding or growth rates due to injuries, could not be accounted for. At least one crab which

Table 2
Survival of crabs captured by Bering Sea trawls. Vitality codes: A = active, M = moribund, D = dead. Total number is weighted by subsampling factors. Letters in parentheses identify variables used in Equations 1 and 2.

Vitality group			Retained subsample			
				Survivors		
Code	Weighted no. (N_v)	Proportion of total	No. kept	No.	Prop. (P_v)	Overall survival (no.)
King crab						
A	307	0.041	134	124	0.925	284
M	3617	0.486	455	158	0.347	1256
D	3521	0.473	28	0	0.000	0
Total	7445		617		0.207	1540
Standard error of estimate					0.010	
Confidence interval (± 2 SE)					0.020	
Confidence range					0.187–0.227	
Tanner crab						
A	154	0.009	1	1	1.000	154
M	5261	0.319	72	47	0.653	3434
D	11083	0.672	1	0	0.000	0
Total	16498		74		0.217	3588
Standard error of estimate					0.018	
Confidence interval (± 2 SE)					0.036	
Confidence range					0.182–0.253	

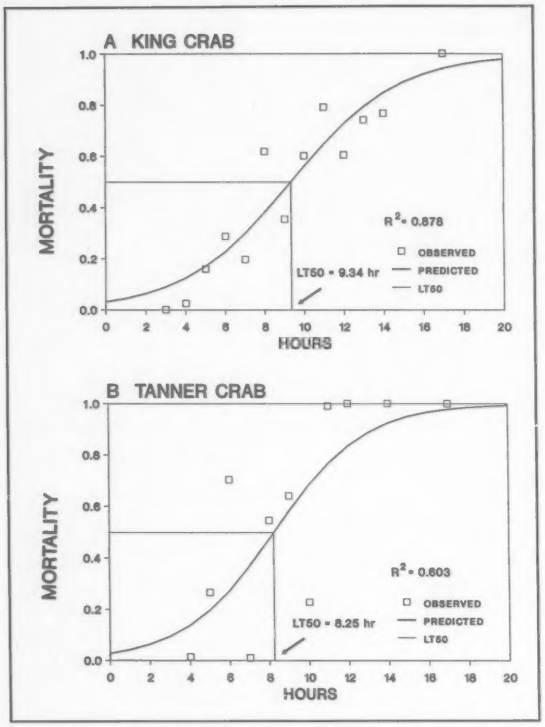

Figure 2

Logistic regression of immediate mortality vs. total time spent in captivity. Crabs were grouped into 1-hour intervals before analysis. (A) 6 113 observations representing 7487 individuals. (B) 4645 observations representing 16 498 individuals. Squares are observed data, solid lines represent predicted values.

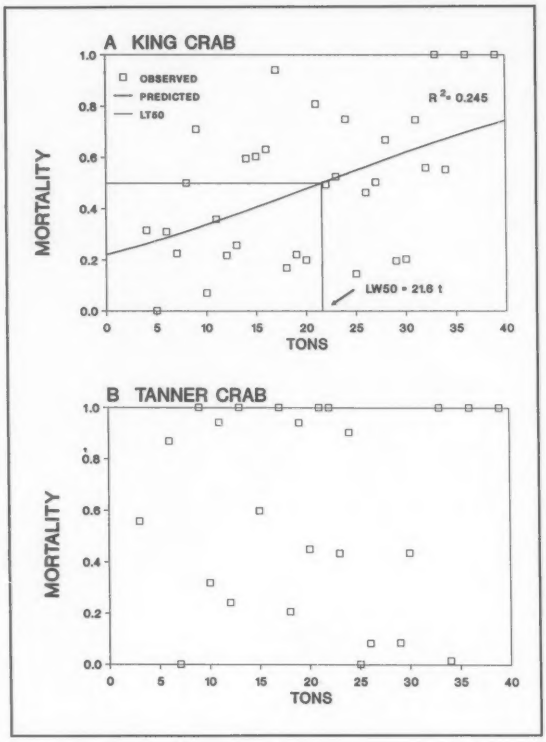

Figure 3

Logistic regression of immediate mortality vs. total weight of catch. Crabs were grouped into 1-t intervals before analysis. Squares are observed data, solid lines represent predicted values, which were incalculable for B.

had been tagged, held for observation, and released was recaptured with its tag still attached. Others may have been recaptured as well, but since most of the tags were removed prior to discarding the crabs, they could not have been identified as recaptures.

Effects of time in captivity and weight of catch

CAPTIME, the total time in captivity (prior to vitality/injury assessment) ranged from 3 to 17 hours (Fig. 2). The logistic fitting procedure indicated a significant relationship ($r^2 = 0.878$, $n = 13$, $\alpha < 0.001$) between CAPTIME and immediate mortality of king crabs (Fig. 2A); the relationship for Tanner crabs (Fig. 2B) was weaker but still significant ($r^2 = 0.603$, $n = 11$, $\alpha = 0.05$). The LT_{50}'s (time required for 50% immediate mortality) were 9.3 hours for king crabs and 8.3 hours for Tanner crabs.

Haul weights ranged from 4 to 39 t ($\bar{x} = 20.4$ t). The relationship between haul weight and immediate mortality for king crabs (Fig. 3A) was poor and non-significant ($r^2 = 0.245$). The relationship for Tanner crabs was so poor (Fig. 3B) that the iterative fitting procedure could not converge on a solution.

Shell conditions

Soft shell or molting crabs (shell condition 1) accounted for only about 1.1% of male king crabs, and <0.1% of females. All other females and most males were hardshell crabs (condition 2). About 9.4% of males were oldshell crabs (condition 3), and virtually all of these were above 100 mm CL. During the NMFS summer EBS survey in June of 1987 (Stevens et al 1987), 2.8% of males were soft or molting and many others were hardshell but recently molted. Immediate survival odds (ratio of survivors to deaths, Fig. 4) increased significantly ($X^2 = 81.63$, $p < 0.001$) with increased shell condition, i.e., hardness, but delayed survival was independent of shell condition ($X^2 = 0.60$, $p > 0.74$).

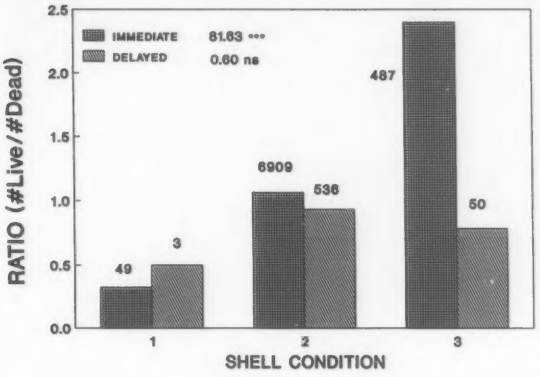

Figure 4

Effects of shell condition on immediate and delayed survival odds of king crabs. Condition coded as 1 = soft, 2 = new hardshell, 3 = old hardshell. Immediate effects are weighted by sample factors, delayed effects are not. *** indicates X^2 value significant at $p<0.001$. Sample size indicated above bars.

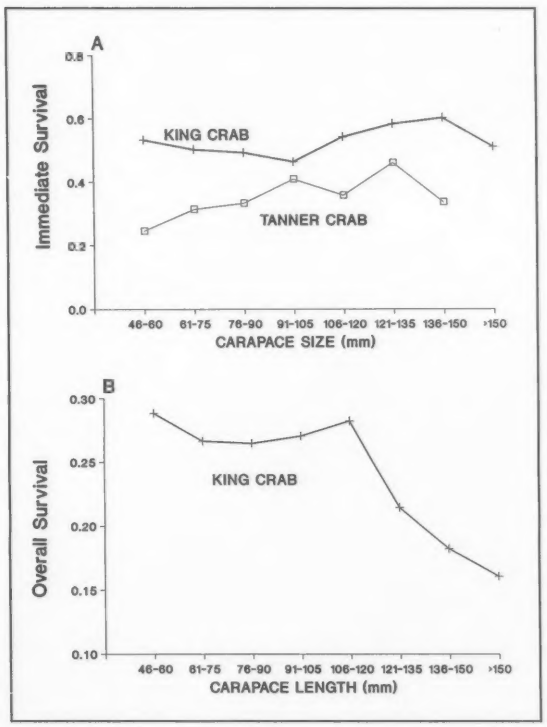

Figure 5

Effects of size on survival. (A) Immediate survival of king and Tanner crabs by 15-mm intervals of carapace length (king crabs) or carapace width (Tanner crabs). Numbers represented by each interval are 226–1520 king crabs and 71–9752 Tanner crabs. (B) Overall survival of king crabs, calculated as the product of immediate and delayed survival estimates.

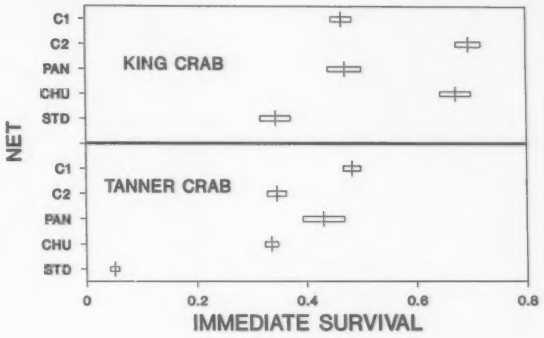

Figure 6

Effect of gear type on immediate survival of king and Tanner crabs. Vertical bar represents the mean; outer ends of box represent upper and lower confidence intervals, defined as $1.96(pq/n)^{1/2}$.

All female and most male Tanner crabs were hardshell (condition 2). Less than 0.3% of males were oldshell (condition 3), and less than 0.01% were softshell (condition 1). Low incidence of softshell and oldshell Tanner crabs prevented contingency table analysis due to too many empty cells.

Size effects

Immediate survival of king crabs did not vary much over the range of sizes captured (Fig. 5A). For Tanner crab, however, immediate survival increased slightly with size. Overall survival of king crabs (Fig. 5B) decreased markedly at sizes above 120 mm CL, mostly as a result of increased delayed mortality. Delayed mortality and overall survival could not be determined for Tanner crabs because of the limited number of observations.

Effects of gear type

Since survival was strongly related to CAPTIME, an analysis of variance was performed to determine if CAPTIME differed between the nets used. No significant differences were found ($F = 0.570$, $\alpha = 0.685$, df = 4181), so any differences in survival between nets can be attributed directly to the nets.

Immediate survival was least for the standard net (STD), for both species (Fig. 6). Nets C2 and CHU produced the best survival for king crabs, whereas C1 and PAN produced better survival for Tanner crabs. Overall, the experimental nets produced no clear differences in survival from the control nets for either species of crab. Extremely poor survival of Tanner crabs occurred in the standard net, and was probably the result of a biased vitality sample, which included

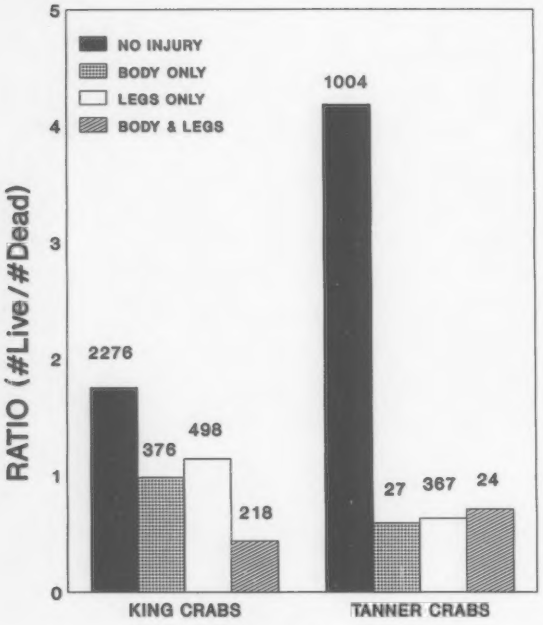

Figure 7

Effects of body and leg injuries on immediate survival odds (ratio of number surviving to number of deaths) of king and Tanner crabs. Sample size indicated above bars. Only injury-assessed crabs were used.

only six tows with this gear type, three of which had large sampling factors and mostly dead Tanner crabs. Delayed mortality was not compared between nets due to limited data.

Effects of injuries

A weighted number of 3368 king crabs and 1421 Tanner crabs were assessed for injuries. Figure 7 shows the survival odds (ratio of number alive to number dead) within each of four combinations of injury types: (1) none, (2) legs only, (3) body only, and (4) legs and body, calculated only for injury-assessed crabs. The majority of crabs suffered no detectable injuries, and had the best survival odds of 1.8 for king crabs and 4.2 for Tanner crabs. The most common type of injury for all crabs was leg injuries, which resulted in survival odds of 1.14 and 0.63 for king and Tanner crabs, respectively. Injuries to the body and combined body and leg injuries were less frequent, resulting in survival odds of 0.98 and 0.44, respectively, for king crabs, and 0.59 and 0.71 for Tanner crabs. Body injuries were more frequent but less serious among king crabs than Tanner crabs and were predominantly broken spines, which are more abundant and prominent on king crabs and thus more likely to be damaged. Body injuries of Tan-

Table 3

Contingency table analysis of interactions between delayed mortality, vitality, and injuries of king crabs. Null hypothesis was that row and column factors were independent. Data were taken only from survival experiment for king crab. Values are observed numbers of crab in each category; numbers in parentheses are calculated expected values or percent of grand total in row or column. All are 2×2 tables with 1 degree of freedom, and all are significant at $p<0.005$ (**).

	Vitality		Row		
Mortality	Active	Moribund	Sum	(%)	X^2 value
Vitality vs. delayed mortality					
Lived	124 (64)	158 (218)	282	(47.9)	138.6**
Died	10 (70)	297 (237)	307	(52.1)	df = 1
Column sum (%)	134 (22.8)	455 (77.2)		Total = 589	
	Injuries		**Row**		
	Uninjured	Injured	Sum	(%)	
Injuries vs. delayed mortality					
Lived	241 (221)	41 (61)	282	(47.9)	16.46**
Died	220 (240)	87 (67)	307	(52.1)	df = 1
Column sum (%)	461 (78.3)	128 (21.7)		Total = 589	
Vitality vs. injuries					
Active	118 (105)	16 (29)	134	(22.8)	9.77**
Inactive	343 (356)	112 (99)	455	(77.2)	df = 1
Column sum (%)	461 (78.3)	128 (21.7)		Total = 589	

ner crabs were typically broken or crushed carapaces which were associated with lower survival. In general, injuries were present in a greater proportion of dead crabs than live crabs. Combined body and leg injuries were most fatal for king crabs, whereas leg-only injuries accounted for the greatest number of dead Tanner crabs. The low survival odds for uninjured king crabs suggests that suffocation in the net or bunkers may have contributed strongly to their mortality.

Contingency table analysis (Table 3) showed that significant interactions occurred between vitality (VIT) and delayed mortality (DMORT; $X^2 = 138.6$), indicating that VIT was an excellent predictor of future survival or mortality for those king crabs held in survival tanks. Similarly, interaction between presence or absence of injuries (INJ) and DMORT ($X^2 = 16.46$) indicated that significantly more injured crabs died than were expected to, and that between VIT and INJ ($X^2 = 9.77$) suggests that injuries were partly responsible for observed vitality levels.

Loglinear analysis with DMORT as the dependent variable, and the interactions of DMORT with both VIT and INJ as independent variables (Table 4) indicated that the overall odds of survival were 2.087:1. These odds were increased by a factor of 4.713 for crabs coded as active (VIT = 1), and by a factor of 1.395 for crabs without injuries (INJ = 1). The total delayed survival odds for active, uninjured crabs equaled 13.73, the product of all three values. Similarly, survival odds for inactive, injured crabs were 0.317, the product of the mean odds (2.087), the odds for inactive crabs (0.212),

Table 4

Parameter estimates and survival odds for each factor in the logit model for king crabs. The dependent factor, DMORT, represents the mean survival odds (ratio of survivors to mortalities) and has no alternative outcome. Each interaction term has two alternative outcomes; alternative 1 represents cells with equal indices, i.e., values for Vitality and Injuries both equal 1 or both equal 2 (Table 5, lines 1 and 4), and alternative 2 represents cells with unequal indices (Table 5, lines 2 and 3). The survival odds for active crabs with no injuries (Vitality and Injuries = 1) is the product of antilogs for DMORT, DMORT × VIT_1, and DMORT × INJ_1, or 13.73. Survival odds are equal to the antilogs of 2(coefficient).

			Survival odds	
Factor	Coefficient	× 2	Alt. 1	Alt. 2
DMORT	0.368	0.736	2.087	
DMORT × VIT	0.775	1.550	4.713	0.212
DMORT × INJ	0.167	0.333	1.395	0.717
Sum		2.619	13.73	0.317

Table 5

Contingency tables used for calculating survival odds (ratio of survivors to mortalities) of king crabs and parameters of logit model. Expected odds are calculated as the product of individual parameters from Table 4. (A) Cells of table shown separately, with expected odds. Numbers in parentheses are factor codes. (B) Cells combined to show overall survival and survival odds calculated using alternative grouping procedures. Procedure 1 used only the criterion of vitality. Procedure 2 simulated the NMFS observer procedure by placing only active, uninjured crabs in category 1. Procedure 3 used only presence or absence of injuries as the criterion.

Cell category		Observed				Expected
Vitality	Injuries	Lived	Died	Proportion surviving	Odds	Odds
A Separate cells						
Active (1)	No (1)	110	8	0.932	13.750	13.727
(1)	Yes (2)	14	2	0.875	7.000	7.051
Morbid (2)	No (1)	131	212	0.382	0.618	0.618
(2)	Yes (2)	27	85	0.241	0.318	0.317
B Combined cells						
1 VIT only						
All active		124	10	0.925	12.4	
All inactive		158	297	0.347	0.532	
2 Observer procedure						
Active, uninjured		110	8	0.932	13.750	
Inactive or injured		172	299	0.365	0.575	
3 INJ only						
All uninjured		241	220	0.523	1.095	
All injured		41	87	0.320	0.471	

Table 6

Comparison of effects of body and leg injuries on immediate mortality of king crabs. (A) Loglinear analysis of immediate mortality (IMORT) as a function of body and leg injuries. Survival odds are equal to the antilog of 2(Coeff.), and are multiplicable. (B) Contingency table of data used for loglinear analysis. Numbers in parentheses are factor codes. Note that expected odds differ from observed odds, but not significantly. $\chi^2 = 3.084$, with df = 1, and $p = 0.08$.

A Parameters of logit model

Factor	Coefficient	× 2	Antilogs Alt. 1	Antilogs Alt. 2
IMORT	−0.017	−0.034	0.966	
IMORT by BODY	0.171	0.341	1.407	0.711
IMORT by LEGS	0.127	0.255	1.290	0.775
Sum		0.562	1.755	0.532

B Contingency table. U = Uninjured, I = Injured

Cell category		Observed				Expected
Body	Legs	Alive	Dead	Percent survival	Odds	Odds
U (1)	U (1)	1428	828	0.633	1.725	1.755
	I (2)	264	234	0.530	1.130	1.054
I (2)	U (1)	185	190	0.493	0.972	0.886
	I (2)	68	152	0.309	0.447	0.532

Table 7

Results of contingency table analyses of effects of types of leg injuries on immediate mortality (IMORT). Null hypothesis tested was independence of each injury type vs. IMORT. Expected ratio of percent live to dead crabs = 1.0 for all cases. Note that totals include uninjured as well as injured crab. ns = not significant at $p = 0.05$. *** significant at $p < 0.001$.

Type of injury	Number alive with injury	Percent of live crabs	Number dead with injury	Percent of dead crabs	Ratio % dead to % live	X^2
King crabs						
Autotomy	35	1.8	36	2.6	1.44	2.48 ns
Distal	284	14.4	313	22.3	1.55	34.86**
Proximal	29	1.5	113	8.1	5.47	88.06***
Total	1967		1401			
Tanner crabs						
Autotomy	47	4.8	123	27.4	5.67	149.85***
Distal	112	11.5	136	30.3	2.63	76.16***
Proximal	11	1.1	35	7.8	6.89	43.63***
Total	972		449			

and the odds for injured crabs (0.717). Alternatively, the log(ODDS) can be predicted as a linear function of each coefficient by substituting these values into Equation 5, e.g., for active, uninjured crabs,

$$\begin{aligned} \ln(f_s/f_m) &= 2(l_D + l_{D*V} + l_{D*I}) \\ &= 2(0.368 + 0.775 + 0.167) \\ &= 2.619 \\ \text{ODDS} &= \exp(2.619) = 13.74. \end{aligned}$$

Thus a 'good' vitality code of 1 was a better predictor of future survival odds than lack of injuries.

Table 5A shows the observed frequencies, percent survival, and survival odds, as well as the survival odds predicted by the logit model, for each combination of factors. Expected odds were calculated as the product of odds for each combination of interaction represented in Table 4. For instance, the expected survival odds for active (VIT = 1), injured (INJ = 2) crabs equalled 7.05, the product of odds for overall survival (2.087), active

crabs (4.713), and injured crabs (0.717). The likelihood ratio chi-squared value, calculated over all categories, was 2.30 with $p = 0.317$, indicating a good fit between the observed and expected survival odds.

In order to compare different methods of crab vitality assessment as tools for predicting future survival, cells of Table 5A were combined. Table 5B shows that using only vitality codes as an indicator of future survival resulted in survival estimates of 0.925 for VIT = 1, and 0.347 for VIT = 2, identical to those shown in Table 2. Simulation of the NMFS observer program procedure resulted in survival estimates which were slightly higher for both categories (0.932 and 0.365, respectively), but otherwise very similar. Use of only data on presence or absence of injuries did not provide adequate information about future survival.

Loglinear analysis was also conducted using immediate mortality (IMORT) as the dependent variable and the interactions of IMORT with body injuries (BODY) and leg injuries (LEGS) as the independent variables (Table 6A). The parameter for mean survival odds was 0.966, or about 1:1. Absence of body injuries increased the odds of survival by a factor of 1.407; their presence decreased survival odds by 0.711. Absence of leg injuries increased survival odds by a factor of 1.290. Coefficients for IMORT × BODY and IMORT × LEGS were not significantly different. Expected odds differed slightly but not significantly ($\chi^2 = 3.084$, df = 1, $p = 0.08$) from observed odds (Table 6B).

Evidence of recent leg autotomy was not significantly associated with immediate mortality of king crabs ($X^2 = 2.48$; Table 7A). However, leg injuries which occurred distal to the autotomy plane were significantly ($X^2 = 34.86$) associated with IMORT, as were those which occurred proximal to it ($X^2 = 88.06$). Proximal injuries had the greatest effect, increasing deaths above the expected proportion by a factor of 5.47. All three types of injuries were significantly associated with IMORT for Tanner crabs (Table 7B). Immediate survival odds, expressed as the ratio of live/dead crabs, decreased significantly with the number of legs injured for both king ($X^2 = 86.5$) and Tanner crabs ($X^2 = 225.3$; Fig. 8A). Delayed survival odds also decreased significantly with the number of injured legs for king crabs ($X^2 = 17.0$), but not Tanner crabs ($X^2 = 4.8$), perhaps due to inadequate sample size for the latter.

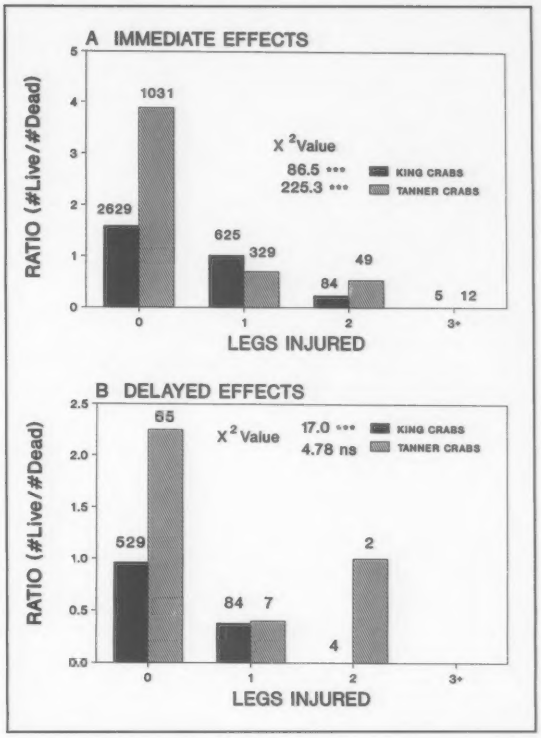

Figure 8

Effects of multiple leg injuries on survival odds of king and Tanner crabs. *** indicates X^2 value significant at $p<0.001$. Sample size indicated above bars.

Discussion

The results of this study show that, although the majority of crabs died as a result of capture incidental to commercial trawling operations, a significant proportion (>20%) can survive the process. The major factors associated with increased crab mortality were shell condition and time in captivity (CAPTIME) prior to recovery. The present study was conducted in August, when both king and Tanner crabs are typically hard-shelled. However, molting for both species usually occurs from January through June, coincident with the season in which most sole trawling occurs in the EBS, so mortality due to molting would probably be greater during the normal fishery. Processing times observed in this study ranged from 0.8 to 12.5 hours, which may have been longer than normal due to the sampling operation, so they probably caused higher than normal mortality. If average processing times for the commercial fishery are less than those observed here, expected mortality would also be less. The study conditions also differed from normal operations in that crabs were retained for several hours after recovery for examination, whereas those recovered during normal operations would have been placed on discard conveyors and returned to sea sooner, probably increasing their survival rates.

For king crabs, the relationship between time in captivity and immediate mortality was strong enough that knowledge of average processing times for a particular trawl fishery could be used to estimate overall survival of crabs. It can also allow estimation of the effects of reduced captivity time on survival. In this study, immediate survival (0.527) and delayed survival (0.472) of king crabs were approximately equal (Table 2). For illustrative purposes we can assume that this equivalency is a general phenomenon, and these two aspects of survival vary proportionally, since increased stress should result in increases in both immediate and delayed mortality. Based on this assumption, the estimated overall survival at the median lethal time of 9.3 hours would be approximately 0.5×0.5 or 0.25, which is very close to the value of 0.21 estimated in Table 2, but differs slightly because the latter was calculated in a stratified manner over all conditions rather than just representing the median lethal time. Overall survival could theoretically be doubled to 50% by reducing CAPTIME such that immediate (and consequently delayed) survival was equal to $0.5^{1/2}$, or 0.71, i.e., by reducing mortality to 1–0.71, or 0.29. Solving the logistic equation (Eq. 3) for X results in:

$$X = X_{50} - \{\ln[(1 - M)/M]\}/r \qquad (3.1)$$

Substituting $0.29 = M$ (as determined above), $9.34 = X_{50}$, and $0.367 = r$ (the latter two values are fitted parameters from the logistic model for king crab survival) results in $X = 6.90$ hours. Thus, for this example, reducing the median total time in captivity from 9.34 to 6.9 hours (a 26% reduction) would increase the immediate and delayed survival rates from 0.50 to 0.71 (a 42% increase), and consequently increase the overall survival to a value equal to the square of immediate survival, $0.71 \times 0.71 = 0.50$, i.e., a 100% increase in overall survival, assuming immediate and delayed survival to be approximately equal, as stated above.

Reduction of CAPTIME, the time crabs spend in the trawlnet or the processing bins, could be accomplished by reducing either towing time, processing time, or both. If towing time cannot effectively be reduced (and may in fact need to be increased to efficiently use the experimental trawls because of reduced fish catch rates) then delay time (between net haulback and delivery to the processing vessel) and processing time (time spent on deck or in the bunkers prior to recovery) should be reduced as much as possible. This could be achieved through better communication and coordination between catcher and processor vessels in order to more evenly distribute deliveries to the processor over time, and reduce or prevent a backup in processing. Towing time may actually contribute less to mortality than processing time, since fish and crabs are less densely packed in the net during towing, and have access to free flowing water. However, neither of these variables (towing or processing time) provided a significant predictive relationship by themselves. Once the codend is recovered on deck, the packing density and pressure within the codend increase greatly and probably contribute substantially to mortality of fish and crabs therein.

Observers placed aboard trawlers by NMFS or the State of Alaska have a variety of tasks to perform, and assessing crab vitality has usually been one of low priority. If one objective were to determine the proportion of crabs that clearly have the best chance of survival, then a two-step process using both vitality and the presence of injuries, such as that currently used by the NMFS observer program, is a better method, as crabs which fell into the "best" category of this scheme exhibited 93.2% survival. Even better predictions could probably be made if degrees of injury (e.g., none, mild, severe) were coded and used to predict survival. However, if the object were to predict survival using the quickest and most efficient method of assessment, then use of vitality alone might be the best choice, as it indicated similar survival (92.5%) for the top category and could be assessed adequately in seconds, whereas a comprehensive assessment for injuries required a deliberate, systematic examination, consuming more time than may be available, given the priority of the task. Even then, some injuries, such as minor cracks in the carapace, were easy to miss.

Despite the quantity of data collected on injury types and severity, there was no clear, unambiguous relationship between injuries and mortality. The overall physical condition of crabs, which could be assessed by activity level, was a better indicator of future survival than injuries. Leg injuries were only slightly more fatal than bodily injuries to king crabs. Both immediate and delayed mortality increased with the number of legs injured, and proximal injuries to legs were more fatal than distal injuries, which was not unexpected since bleeding from the coxa or basi-ischium (leg segments which are proximal to the autotomy plane) would likely be more difficult for the crab to stop than bleeding from a more distal segment, which could be autotomized at a later time. In our experience, though, it was uncommon for crabs that had injured legs at the time they were examined to autotomize them in the live tanks. If autotomy had not occurred soon after the injury, and prior to examination, it was less likely to do so after a day or two. However, this is a subjective observation and was not documented, because injuries were not reassessed prior to release. The poor relationship between injuries and death suggests that other factors, such as exposure or suffocation, may have played a significant role in determining survival of crabs.

In an attempt to simulate the effects of culling crabs in the directed, winter-season pot fisheries, Carls and O'Clair (1990) documented the effects of exposure of ovigerous female king and Tanner crabs to various combinations of time and air temperature (max. 40 min. at −19°C). They found that both mortality and righting time were inversely proportional to exposure, expressed in terms of degree-hours, but neither response occurred in air temperatures above 0°C. Their conditions contrasted with this experiment; although water and air temperatures were not recorded, 30-year mean August seawater temperatures in the area where this experiment was conducted have been 2–5°C on bottom and 8–9°C at surface (Ingraham 1983), and air temperatures were probably above 10°C, so no negative degree exposures occurred. However, during the winter trawl fishery such exposures might occur, although most crabs would be insulated by the surrounding catch in the net or processing bins.

Carls and O'Clair (1990) also found that exposure-related mortality of king crabs was delayed, occurring 16–128 days after exposure, and was usually associated with ecdysis; in contrast, 50% of their Tanner crab mortality occurred within the first 24 hours. Although crabs were not retained over 48 hours in the present experiment, and no ecdysis occurred, exposures were not as severe either.

Location of leg breaks was found to be related to mortality of stone crabs *Menippe mercenaria* by Simonson and Hochberg (1986). They studied the effects of exposure and claw breakage on survival of stone crabs and found that breakage on either side of the breakage plane resulted in significantly higher mortality than breaks on the plane. Mortality also increased with severity of the break, and length of exposure, from 2 to 6 hours. Severity of breaks also increased with exposure time prior to breakage. In their study, claw breakage was intentional rather than accidental, as fishermen remove the claws for sale and return the live, clawless crab to the sea.

Crabs subjected to trawl capture and subsequent release probably also suffer some sublethal effects, but they could not be documented in this study. Brown and Caputi (1985) studied the effects of exposure and leg loss on growth of sublegal rock lobsters *Panulirus cygnus*, and found that exposure for periods of 15, 30, and 60 minutes resulted in decreased growth at the next molt of 0.8–2.3 mm, or 1.2–3.3% of carapace length. In addition, the growth increment was reduced by 0.48 mm, or about 0.7%, for each appendage missing. Carls and O'Clair (1990) also found that female king crabs exposed to subzero air temperatures showed decreased growth at subsequent molts. Other sublethal effects included reduced feeding rates and increased limb autotomy by female Tanner crabs.

The recapture of a tagged and released crab indicates that such multiple captures of discarded crabs may be common in this type of intensive fishery. Recaptured crabs would probably have lower survival rates than crabs captured and released only once, due to the cumulative effects of stress and injuries. However, there is no evidence suggesting that the rate of recapture during the experiment differed from the normal conditions of the commercial fishery, so the calculated survival rates may adequately incorporate any effects of recapture.

Smith and Howell (1987) studied the effects of trawl capture on American lobsters *Homarus americanus* in Long Island Sound and found that the incidence of damage varied seasonally from 0 to 14%, and was greater during months when molting was occurring. Immediate plus delayed mortality ranged from 1% to 21%, depending upon season also. In contrast to this report, they found that uninjured lobsters, and those with autotomized claws rarely experienced delayed mortality, and that seasonally warm seawater temperatures were associated with increased delayed mortality independent of damage. The conditions to which lobsters were exposed differed greatly from those encountered by king crabs, however, as the lobsters were commonly sorted out of the catch in less than an hour, as opposed to times of 3–17 hours for crabs in this study.

The effect of discarding crab via conveyor belts and discard chutes from the factory was not examined, and could inflict further injury upon crabs via entanglement in machinery or damage upon impact with the water surface, 3–6 m below the discard chute.

The estimated catch of 88000 red king crabs and 751000 Tanner crabs *C. bairdi* by the Bering Sea JV fishery in 1988 (Berger and Weikart 1989) amounted to 0.22% and 0.11% of the total estimated abundance of those two species, respectively, in the Bering Sea that year (Stevens et al. 1988). Even though the amount of bycatch in the domestic fishery is unknown, it is unlikely that the total bycatch exceeded 0.5% of the population for either species, largely as a result of restrictions on bycatch. Removals of this magnitude are well below the ability of the NMFS crab survey to detect, and probably have no significant biological impact. The possibility of additional, unseen mortality of crabs due to trawling has largely been discounted by submersible studies (West 1987, Highliners Association 1988) in which the observed trawls made little or no contact with the sea bottom, caused no observable injuries to crabs contacted, and no injured or dead animals were observed in the wake of the net.

Nevertheless, the issue of bycatch mortality is of great concern to the fishing industry, and the North Pacific Fishery Management Council has developed a

policy of reducing bycatch mortality as much as possible. To that end, the most useful results of this study were, first, that crab mortality increased with CAPTIME, so reduction of CAPTIME should be a high priority. Second, reduction of king (and probably Tanner) crab mortality could be achieved by conducting the trawl fishery during periods of the year when molting activity is at a minimum.

Summary

1 Over 50000 crabs were measured during the study. Vitality was recorded for over 10000, injuries for 3353, and delayed mortality for 691.

2 Overall survival was estimated to be 21% (±2.0%) for king crabs and 22% (±3.6%) for Tanner crabs.

3 Overall survival of king crabs declined at sizes above 120 mm CL. Overall survival could not be determined for Tanner crabs, but immediate survival showed a slight increase with size.

4 Immediate mortality of king and tanner crabs increased in direct proportion to time in captivity, but was poorly related to weight of the catch.

5 Immediate survival odds for king crabs increased significantly with shell age.

6 No clear difference in survival was apparent between the net types for either king or Tanner crabs.

7 Delayed mortality was shown to be dependent on both vitality and injuries, with vitality being the best predictor. Observation of injuries did not contribute substantial additional information concerning future (48-hour) survival.

8 Leg and body injuries contributed about the same amount to immediate mortality, but mortality increased with number of legs injured, and injuries to leg segments proximal to the autotomy plane were more serious for king crabs but not for Tanner crabs.

Acknowledgments

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Differential Growth Among Cohorts of Age-0 Weakfish *Cynoscion regalis* in Chesapeake Bay*

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Abstract.– Age-0 weakfish *Cynoscion regalis*, were sampled from the Chesapeake Bay–York River estuary in 1983 and 1984 to test for the existence of multiple cohorts and compare growth rates. In both years juveniles were first collected in the estuary in late July, were significantly more abundant from August to mid-October, but were uncommon by the end of October. Significantly more weakfish were collected in 1983 than in 1984. Daily ages were determined based on scale circuli. Cohorts were separated by local minima in birthdate distributions: cohort 1 hatched before 16 July 1983, cohort 2 (16 July–15 August 1983), cohort 3 (15 August–9 September 1983), cohort 4 (5 May–20 June 1984), and cohort 5 (5 July–1 September 1984). Compared with other cohorts, groups 1 and 4 had significantly slower growth rates (0.83 and 0.84 mm/day, respectively), while cohort 5 had a significantly faster growth rate (1.09 mm/day), and cohorts 2 and 3 were intermediate (both at 0.96 mm/day). Weakfish juveniles were transient and migrated up the estuary as they grew, as indicated by cohort and age distributions over stations and dates. Also, cohorts appeared to partition the estuary; for example, cohort 1 was more common up the estuary compared with other cohorts. The existence of multiple cohorts with significantly different growth rates and apparent differential habitat use suggests that the juvenile stage of weakfish may show high variability in survival, and the presence of multiple cohorts within a single year-class must be considered in the estimation of juvenile recruitment to the adult population.

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A common assumption of early-life-history studies of fishes has been that the most critical period for survival occurs during egg and larval stages, thereafter juvenile fish show fairly constant growth and mortality rates (Cushing 1975, Williams 1983, Hewitt et al. 1985, Victor 1986). However, postmetamorphic survival may be highly variable and we may need to extend the critical survival concept to include the juvenile stage of fishes to better understand year-class variability (Walline 1985, Eckert 1987, West and Larkin 1987). The existence of multiple cohorts within age-0 fishes may help explain variable annual survival of juvenile fishes (Buchanan-Wollaston and Hodgson 1929, Cooper 1937, Lambert and Ware 1984). Survival is difficult to estimate without information on residency time, but growth rate can be used as an indicator of potential survival because it is an integrator of most other environmental factors. For example, those individuals that grow the fastest will increase their chances of survival because they grow through the size range vulnerable to predators at a faster rate (Tonn and Paszkowski 1986, Post and Prankevicius 1987, Post and Evans 1989). Faster growth also implies that they are more physically fit, e.g., larger individuals may be able to survive overwinter stress better than smaller individuals (Conover and Ross 1982, Takita et al. 1989).

The key to evaluating variation in growth rates among age-0 fishes is the ability to age young fish. Larval and juvenile fishes have been assigned daily ages by length-frequency analysis, a somewhat imprecise method (MacDonald 1987), or by counting microincrements in otoliths (see reviews: Campana and Neilson 1985, Jones 1986). Daily aging of juvenile weakfish *Cynoscion regalis*, by otolith microincrements was unreliable (Szedlmayer 1988), but a new method of counting circuli in scales appears promising (Szedlmayer et al. In press). The present study uses this new method to test for multiple cohorts within age-0 weakfish, and to estimate growth rates and differential habitat use by fish collected in the Chesapeake Bay–York River estuary, Virginia.

*Contribution no. 1604, Virginia Institute of Marine Science, College of William and Mary.

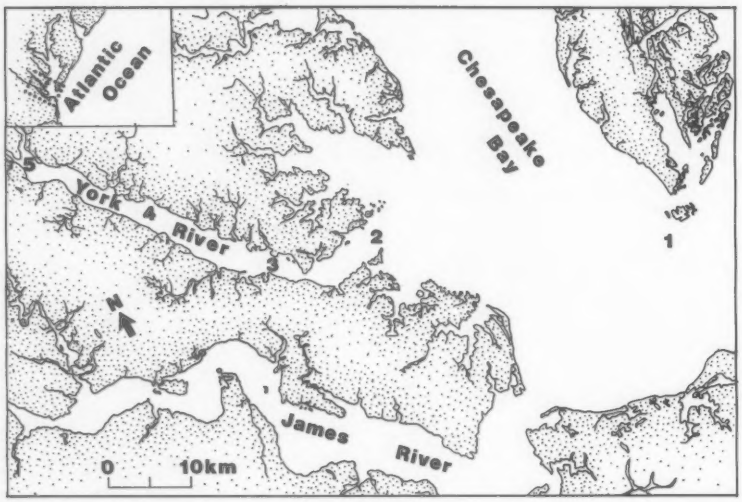

Figure 1
Station locations for age-0 weakfish collections in Chesapeake Bay–York River, VA. Station 1 (0 km, bay entrance), station 2 (30 km up estuary), station 3 (45 km up estuary), station 4 (63 km up estuary), and station 5 (75 km up estuary).

Materials and methods

Juvenile weakfish were collected at night (Leber and Greening 1986) with an otter trawl (4.9 m, 19-mm mesh wings, 1.5-mm codend). In 1983, collections were made weekly at four stations in the York River estuary, Virginia, from 12 July to 26 October: stations 2, 3, 4, and 5; 30, 45, 63, and 75 km up the estuary from the Bay entrance, respectively (Fig. 1). Station 1 was added at the mouth of Chesapeake Bay in 1984, while collections at Station 4 were discontinued (Fig. 1). In 1984, collections were made every 2 weeks from 21 June to 16 November. Repetitive, 2-minute trawls were made at each station until 30 fish were captured or until 6 tows were completed. Salinity and temperature were recorded with a Beckman conductivity meter at the bottom at each station.

Weakfish were stored in 70% ethanol. Standard lengths of preserved fish were recorded with calipers to the nearest 0.1 mm. At least three scales were taken from just below the midbody lateral line curve (usually five) and circuli were counted according to Szedlmayer et al. (In press). When three scales could not be taken, the fish was not used. The highest scale circuli counts from individual weakfish were used for age estimations. Age was estimated, based on daily scale circuli counts, plus a 26-day estimate of the time delay from hatching to first circulus formation. Also, if fish were <14 mm SL (prior to scale formation), age was estimated by quadratic regression of size on age based on laboratory-reared fish (for validation of daily circuli deposition and further details of this method, see Szedlmayer et al. In press). Subsequently, birthdates were backcalculated by subtraction of estimated age from date of capture. Birthdate frequency distributions were smoothed with a 3-day moving average. Cohorts within a year-class were identified by local minima in the birthdate frequency distributions (Graham and Townsend 1985). After separation of fish into their respective cohorts, growth rates were estimated by linear regression of standard length on age. Migration patterns within the estuary and differential habitat use by cohorts were suggested by abundance modes over stations and collection dates, mean ages by stations, and cohort-specific age-frequency distributions over stations and collection dates.

A 0.05 level of significance was used for analysis of variance and covariance. Nonparametric analysis of variance by ranks of main effects (year, station, date) was used to test for abundance differences (catch-per-unit-effort = number/2-minute trawl tow). Analysis of covariance was used to test for significant differences in growth rates among cohorts. Analysis of variance was used to test for age differences among stations, pooled over dates. After significance was determined, Student-Newman-Keuls test was used to show specific differences at a 0.05 level of significance or a 0.10 level if a type II error resulted at the former level (Zar 1984).

Results

Salinity variation was associated with station, while temperature variation was associated with season. As

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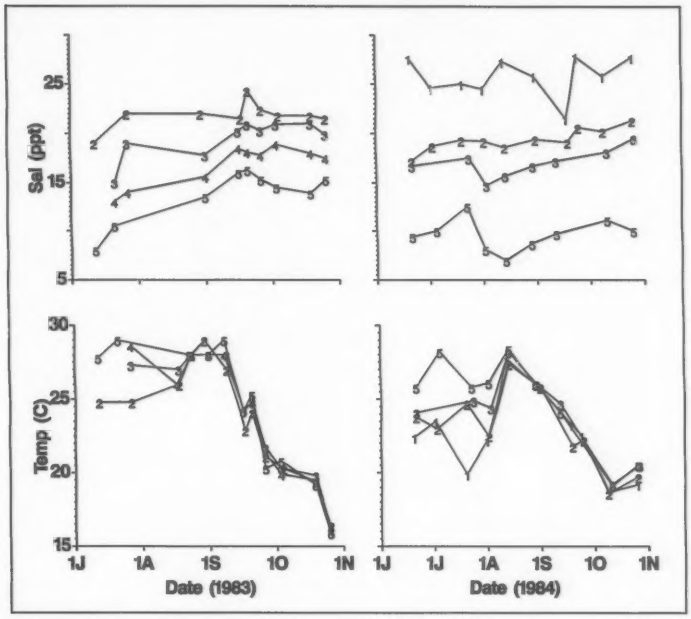

Figure 2
Salinity and temperature in Chesapeake Bay–York River, VA, from all collections, 1983 and 1984. Numbers on each line refer to station and mark data points.

expected, salinity was highest at station 1, and decreased up the estuary. Salinity was slightly higher at stations 2 through 5 in 1983 compared with 1984 (Fig. 2). Little difference was detected in temperature among stations, except in June and July 1984, where temperatures were 4–5°C warmer at the upper estuary stations. Seasonally, temperature ranged 16–29°C in 1983, and 18–29°C in 1984 (Fig. 2).

Weakfish catch-per-unit-effort was significantly greater in 1983 than in 1984 (Table 1; Fig. 3). Seasonally, fish were uncommon in July samples, significantly more abundant in samples taken from mid-August to mid-October, but by the end of October were few in number. No significant differences in catch-per-unit-effort were detected among stations. Lack of replication in some cells (i.e., one 2-minute tow resulted in >30 weakfish) prevented testing for interaction effects between station and date. However, although not statistically significant, there was an apparent pattern: in both years fish were first abundant down estuary, and as the season progressed became more abundant further up the estuary (Fig. 3).

In 1983, 845 fish were aged out of 993 collected, and in 1984, 361 fish were aged out of 571 collected, by the scale circuli method. An additional 98 fish were <14 mm SL (prior to scale formation), and ages were estimated by applying a quadratic regression of known age on standard length from laboratory-reared weakfish (Szedlmayer et al. In press).

Table 1
Juvenile weakfish CPUE (no./2-minute tow) from the Chesapeake Bay and York River, VA, based on three-factor (main effects only) nonparametric ANOVA by rank abundance. Student Newman Keuls test (SNK) was used to show specific differences, denoted by different letters (0.05 level).

Source of variation	df	MS	*F*	*P>F*
Year	1	5138.7	16.90	0.0001
Station	4	389.4	1.28	0.2870
Date	7	1216.4	4.00	0.0012
Error	61	303.7		

	CPUE	Trawls	SNK-test
Date			
16–29 July	1.2	20	C
30 July–12 Aug.	0.8	16	C
13–26 Aug.	5.0	60	A B
27 Aug.–9 Sept.	7.1	51	A
10–23 Sept.	8.5	37.5	A
24 Sept–7 Oct.	5.1	52	A
8–21 Oct.	4.4	46	A B
22 Oct.–4 Nov.	1.6	49	B C
Year			
1983	6.5	152.5	A
1984	3.2	179	B

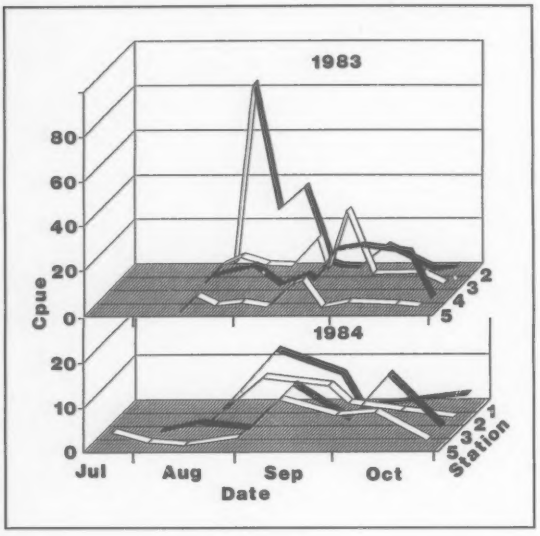

Figure 3

Standardized abundance of age-0 weakfish (CPUE = number/2-minute tow) by station and date in Chesapeake Bay–York River, VA.

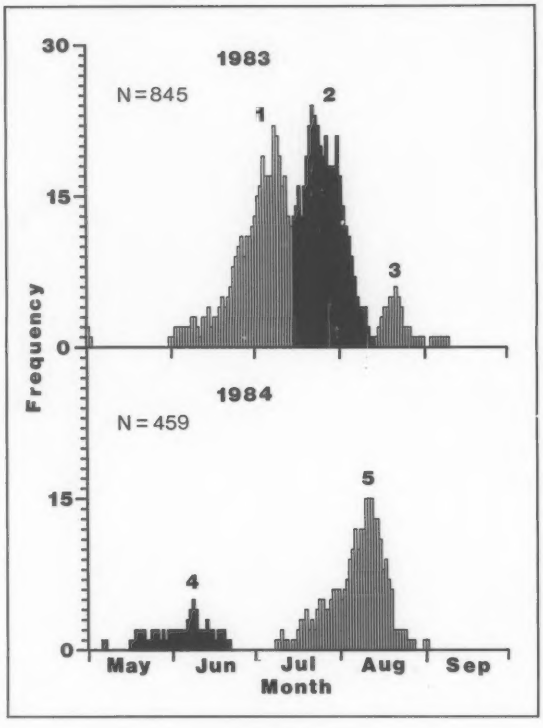

Figure 4

Birthdate frequency distribution of age-0 weakfish cohorts in Chesapeake Bay–York River, VA, based on a 3-day moving average. Numbers at the peaks of the distributions refer to cohorts (separated by open and shaded bars).

Multiple cohorts were apparent in both years. The birthdate frequency distributions showed three cohorts in 1983, and two cohorts in 1984 (Fig. 4). Cohorts were defined in 1983 as follows: cohort 1 hatched before 16 July, cohort 2 between 16 July and 15 August, and cohort 3 after 15 August. Another cohort may have been present in 1983 before 18 June, but these fish were relatively few in number and subsequently pooled with cohort 1. In 1984 two cohorts 4 and 5 were defined as those that hatched before 30 June and those after, respectively (Fig. 4).

Weakfish growth rates were significantly different among cohorts within years, and between years (Table 2). Cohorts 1 and 4, both early-season cohorts, had the lowest growth rates and were not significantly different from each other. Cohorts 2 and 3 had intermediate growth rates, and cohort 5 had the fastest growth rate compared with all other cohorts (Table 2).

After separation of individual weakfish into their respective cohorts, a similar pattern of movement by each cohort was apparent: up the estuary with age and season (Figs. 5, 6). For example, the youngest fish in cohort 2 were first most abundant in the lower estuary (stations 2 and 3), and as the season progressed older fish from this cohort were more abundant up the estuary at the same location where few individuals of this cohort were collected earlier (station 4 in August vs station 4 in September 1983; Fig. 5). Cohort 4 showed the only difference from the above migration pattern.

Table 2

Growth rates (mm/day) of individual age-0 weakfish cohorts. Analysis of covariance of standard length on age with cohort as the covariate (0.05 level). Student Newman Keuls test (SNK-test) was used to show specific differences, denoted by different letters (0.10 level).

Source of variation	df	MS	F	$P>F$
Cohort	4	20178.39	1597.8	0.0
Age	1	448840.88	35540.4	0.0
Age * Cohort	4	1686.94	133.6	0.0
Error	1294	12.63		

Cohort	Growth rate	R^2	N	SNK-test
1	0.83	0.95	383	A
2	0.96	0.96	405	B
3	0.96	0.94	57	B
4	0.84	0.96	75	A
5	1.09	0.98	384	C

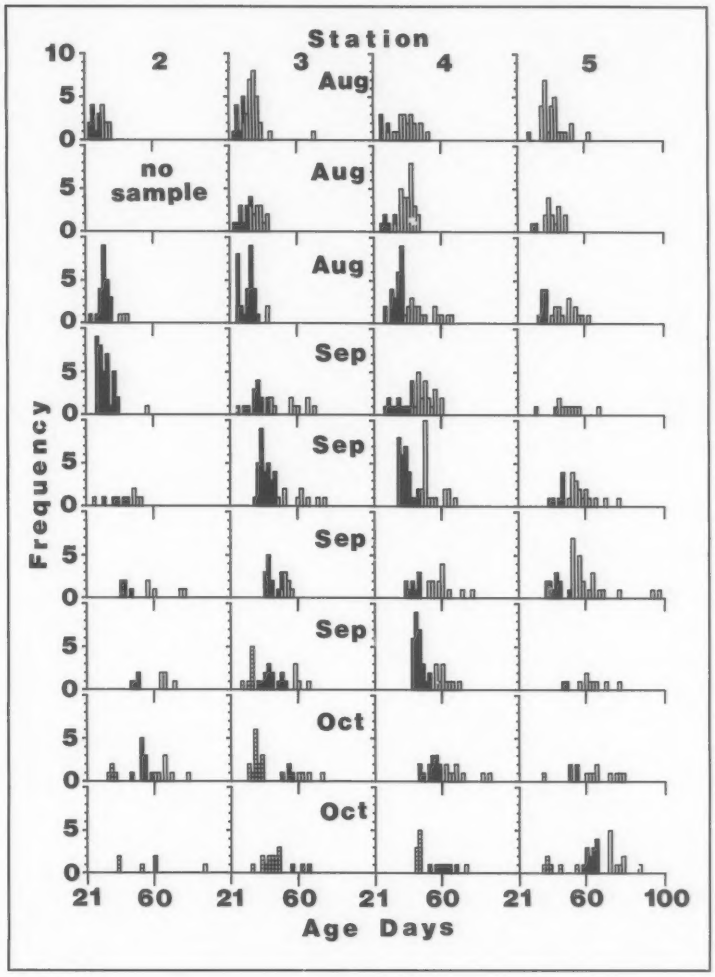

Figure 5
Age of weakfish estimated from scale circuli for 1983, versus frequency (number/2-minute tow), by station, date, and cohort in Chesapeake Bay–York River, VA. Cohort 1 = open bars, cohort 2 = solid bars, and cohort 3 = cross-hatched bars.

The earliest recruits in cohort 4 were first collected at the upper estuary station (5), then appeared to spread down the estuary in subsequent collections (Fig. 6). An up-the-estuary movement with age pattern was also supported by the mean ages associated with each station, because weakfish were significantly older as the distance from the Bay mouth station (1) increased (Table 3), and by an increase in total catch-per-unit-effort up the estuary with season (Fig. 3). Different cohorts appeared to segregate habitats. In 1983, cohort 1 was more common further up the estuary compared with other cohorts, while cohort 2 dominated the middle habitats (Fig. 5). Cohorts 3 and 4 were lower in abundance and it is difficult to suggest a pattern, while cohort 5 appeared dominant at all stations after August 1984 (Fig. 6).

Discussion

To our knowledge this is the first clear identification of multiple age-0 weakfish cohorts, and they showed significantly different growth rates and appeared to partition habitats. Earlier, Massmann (1963) suggested the existence of age-0 multiple cohorts from bimodal length-frequency distributions, but did not examine growth rates or differential habitat use. Except for two early studies (Buchanan-Wollaston and Hodgson 1929, Cooper 1937) reports of multiple cohorts in the juvenile stage of fishes are few (Shlossman and Chittenden 1981, DeVries and Chittenden 1982, Crecco and Savoy 1985, Kumagai et al. 1985, Eckert 1987, Isely et al. 1987, Wicker and Johnson 1987). This may be because of the difficulty of aging juvenile fishes (Geffen 1986,

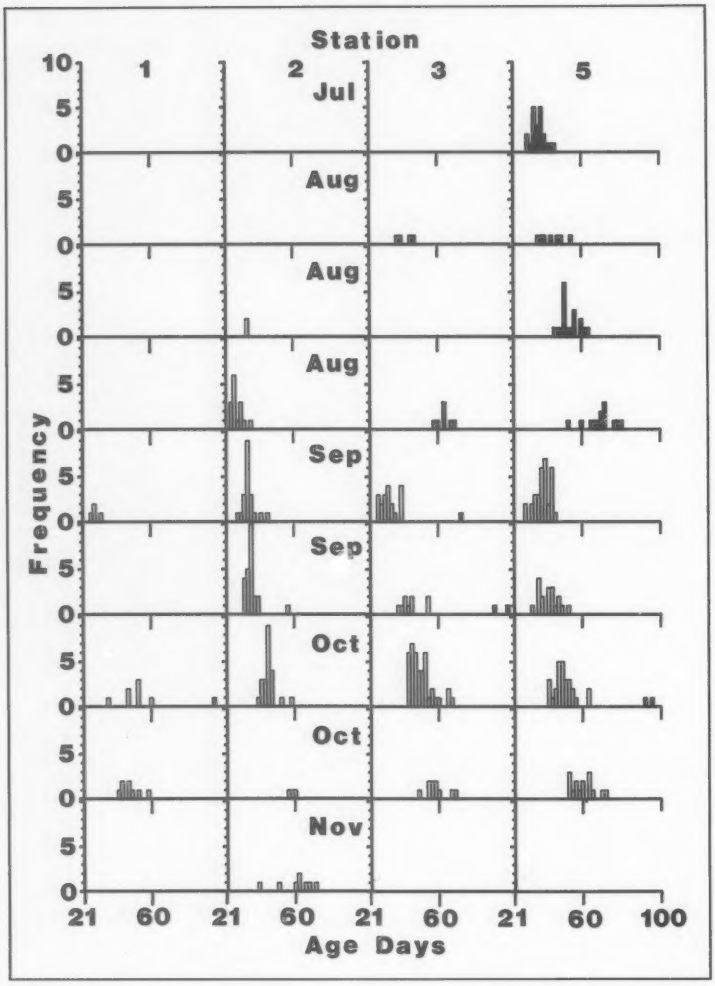

Figure 6
Age of weakfish estimated from scale circuli for 1984, versus frequency (number/2-minute tow), by station, date, and cohort in Chesapeake Bay–York River, VA. Cohort 4 = solid bars, cohort 5 = open bars.

Table 3
Comparison of weakfish age by station, pooled over dates, based on ANOVA (0.05 level). Student Newman Keuls test (SNK-test) was used to show specific differences, denoted by different letters (0.05 level).

Source of variation	df	MS	*F*	*P>F*
Station	4	37126.0	123.6	0.0001
Error	1299	300.3		

Station	Age	*N*	SNK-test
1	26.1	104	A
2	50.2	248	B
3	57.1	346	C
4	61.8	279	D
5	66.8	327	E

Essig and Cole 1986, Jenkins 1987, Post and Prankevicius 1987), or that fewer studies have examined postmetamorphic life stages because juvenile survival after metamorphosis was considered relatively constant compared with larval stages (Cushing 1975, Victor 1986). Constant growth and mortality in postmetamorphic juveniles have been questioned; for example, Wicker and Johnson (1987) showed a large increase in the rate of mortality in age-0 largemouth bass *Micropterus salmoides* when juveniles shift from an invertebrate to fish diet. Van der Veer and Bergman (1987) suggested that mortality due to predation by shrimp *Crangon crangon* on newly settled juvenile plaice *Pleuronectes platessa* may be significant and thus account for the difficulty of predicting year-class abundance based on egg and larval surveys. However,

studies of American shad *Alosa sapidissima* suggested that year-class strength is established before the juvenile stage (Crecco et al. 1983, Crecco and Savoy 1984, Crecco and Savoy 1985). Consequently, the importance of critical periods during the juvenile stage may be species-specific. Because several age-0 cohorts of weakfish showed variable growth rates and distribution, survival of the juvenile stage of this species should not be assumed to have a constant rate.

Different population parameters among cohorts are difficult to relate to salinity and/or temperature differences observed among stations. First, juvenile weakfish are transient, as observed over the present study area and in earlier studies (Harmic 1958, Massman 1963, Chao and Musick 1977, Shepherd and Grimes 1983), and until accurate residency times can be estimated it may be ineffective to ascribe cohort differences to particular habitat parameters. Second, other factors not measured in the present study, e.g., prey abundance, turbidity, currents, and predation may also be linked to cohort differences.

In comparison with other juvenile fish, age-0 weakfish appear to grow at an average rate. Juvenile growth rates derived from length frequencies for other sciaenid fishes were similar to our estimates for weakfish: *C. arenarius* (~1 mm/day, Shlossman and Chittenden 1981), *C. nothus* (0.8–1.3 mm/day, DeVries and Chittenden 1982). Shenker and Olla (1986) provide estimates of juvenile fish growth rates ranging from a low of 0.26 mm/day (*Sebastes melanops*) to a high of 4.7 mm/day (*Coryphaena hipporus*). Other growth rate estimates of juvenile fishes include: 1.5 mm/day for *Anoplopoma fimbria* (Boehlert and Yoklavich 1985), 1.0–1.3 mm/day for *Chanos chanos* (Kumagai et al. 1985), and 1.1 mm/day for *Alosa sapidissima* (Crecco and Savoy 1985).

The ecological advantage of extended spawnings that result in multiple cohorts within a single age-0 year-class can be thought of as a "hedged bet" strategy that spreads age-0 production over time to take advantage of a variable environment (Lambert and Ware 1984). However, distinct cohorts within age-0 fish can also result from environmental factors acting on a single spawning effort; for example, through variation in prey availability (Timmons et al. 1980, Keast and Eadie 1985, Wicker and Johnson 1987), or a combination of biotic and abiotic factors (Lambert 1984, Crecco and Savoy 1985). However, previously published information indicates that the multiple cohorts observed in the present study probably resulted from multiple spawnings. Shepherd and Grimes (1984) showed that large weakfish "tiderunners" 55–80 cm enter the Delaware Bay estuary in the spring and spawn. In the summer these were replaced by 25–35 cm gravid weakfish. Harmic (1958) showed a repeating pattern of multiple spawning over 3 years, where a peak of egg abundance occurred in mid-June, followed by a conspicuous gap, and another peak in mid-July.

In summary, the present study showed that multiple cohorts exist within the age-0 year-class of Chesapeake Bay-York River weakfish. These cohorts showed significant differences in growth rates and appeared to partition habitats. Consequently, population studies directed at predicting year-class strength from juvenile surveys need to consider the potential for age-0 cohort variability.

Acknowledgments

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Growth per Molt of Male Snow Crab *Chionoecetes opilio* from Conception and Bonavista Bays, Newfoundland

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Abstract.–Over 6000 male snow crabs were tagged during a 6-year period in Conception Bay, Newfoundland, in order to estimate the increase in size at the time of molting. Ninety-two animals were recaptured which had usable information on growth increments. Based on the amount of growth, we hypothesized that 20 of these had molted once while the remainder molted twice. Two lines of evidence support this interpretation. First, animals in the group presumed to have molted twice were at liberty on average twice as long as those presumed to have molted once. Second, a regression line fitted to data on single-molters predicted the size after two molts in close agreement with a regression line fitted to data on double-molters. A nonlinear regression model was developed to estimate the parameters of the relationship between post- and pre-molt sizes using the combined data set for single and double molters. The method was also generalized to account for a quadratic relationship between post- and pre-molt size. For crabs in the size range 80–110 mm carapace width, the predicted size after molting in mm is equal to $7.398 + 1.038 \times$ pre-molt size. A similar study conducted in Bonavista Bay, Newfoundland, yielded growth information for 18 animals. The molt increments appear similar to those observed from Conception Bay.

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The snow crab *Chionoecetes opilio* has supported extensive commercial fisheries on both the Atlantic and Pacific coasts of North America since the 1960s (Elner and Bailey 1986). Snow crabs are also commercially exploited in Japan. Only the males are harvested in North America because females never attain commercially acceptable sizes. Efforts to manage the resources have been hampered by a lack of detailed life-history information. This is because the crabs are found in deep water (50–700 m) and are thus difficult to study.

Information on growth of snow crabs is required for effective management for at least three reasons: (1) for incorporation in a yield-per-recruit model, (2) to forecast the biomass available to the fishery from size-specific, pre-season biomass estimates, and (3) to interpret size-frequency distributions. Although growth can be studied in the laboratory, there is no guarantee that the observed growth will reflect what happens in free-living populations. Consequently, there is a need to estimate growth parameters from field data.

There have been some tagging studies of snow crab growth, but the reported results were either of a preliminary nature or were unsatisfactory due to tag retention problems (McBride 1982, Taylor 1982, Bailey and Dufour 1987). Improvements in tagging methods (Hurley et al. In press) have made field studies feasible.

Growth of crustacea is often estimated by studying two components: the increase in size at the time of molting (molt increment) and the timing of molting (either the intermolt period or the proportion molting in a given season). Recent work by Moriyasu and Mallet (1986) and O'Halloran and O'Dor (1988) has provided a method for estimating the proportion of the population that will molt in a given time period. In this paper, we concentrate on the problem of estimating the size-specific molt increment of snow crabs in Conception and Bonavista Bays, Newfoundland, from mark-recapture data consisting of the size at the time of tagging, the size at recapture, and the time at liberty.

Conception and Bonavista Bays are deepwater bays on the Northeast coast of Newfoundland (maximum depth 295 m in Conception Bay; 412 m in Bonavista Bay). Commercial fishing grounds for crabs exist at depths exceeding 180 m. The bottom type in these areas is predominantly mud or muddy sand with mean bottom temperatures ranging from -1.3 to $0.5°C$. Since the mid 1970s both areas have experienced high levels of commercial crab fishing effort (Taylor and O'Keefe 1987). While aggregations of crabs may be found at depths <180 m, the deeper commercial fishing grounds appear to have the soft substrate necessary for snow crab molting.

Figure 1
Map of Newfoundland, Canada, showing the location of Conception Bay (lower box) and Bonavista Bay (upper box).

Materials and methods

From 1979 to 1984, nine research cruises were made to Conception Bay, Newfoundland, Canada (47°30′N, 53°W, Fig. 1), to tag 6296 male snow crabs, size range 56–135 mm carapace width (CW). An additional 2253 male crabs, size range 45–125 mm CW, were tagged during four cruises to Bonavista Bay, Newfoundland (48°50′N, 53°20′W), from 1979 to 1984.

Crabs were captured using Japanese-style conical traps baited with squid *Illex illecebrosus* and set in longlines of twelve traps at depths ranging from 110 to 285 m. Traps were hauled after soaking for 24 hours.

Tagging was conducted in a manner designed to minimize mortality. Traps were spaced approximately 40 m apart, which allowed us to tag crabs from the trap on deck while the other traps remained in the water. Before tagging, we examined each animal and discarded any that appeared injured. Carapace width was measured to the nearest millimeter using vernier calipers. Animals were tagged with a T-bar tag (Floy Tag Mfg. Co., Inc., Seattle, WA 98105) and immediately released on location. Details of the tagging procedure are described in Hurley et al. (In press). Tags were inserted in the posterior ecdysial suture (epimeral line) which was made visible by applying gentle upward pressure to the carapace. The tagging location was 2–6 mm from the right coxopodite of the last walking leg. Before releasing the crab, the end of the tag was given a gentle tug. If the tag appeared loose, it was removed and the animal was discarded. To determine measurement errors, one biologist measured 90 animals three times in blind trials. The animals ranged in size from 63 to 124 mm. Recaptured animals were obtained mostly from commercial fishermen. Only animals that were examined by a staff biologist were used in the analysis.

Results and discussion

Repeated measurements by a biologist of a group of crabs were always within 1 mm of the mean for each animal. Workers studying other species of large crustacea have suggested that measurements can be

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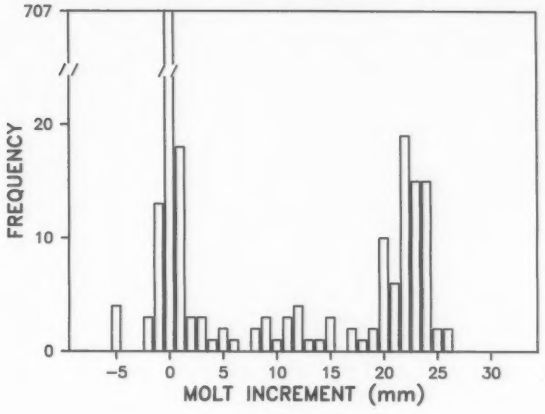

Figure 2

Frequency of occurrence of growth increments for recaptures of *Chionoecetes opilio* from Conception Bay.

precise to within 3 mm (Restrepo 1989, Hunt and Lyons 1986, Little 1972). If measurement errors occur at both the time of tagging and the time of recapture, then errors as large as 5 or 6 mm might be encountered.

Conception Bay

We recovered 850 tagged animals from Conception Bay. Of these, 751 had measured increases in size of 3 mm or less; three had increases of 4–5 mm; the remaining 93 animals had increases of at least 6 mm (Fig. 2). None of the three animals with molt increments of 4 or 5 mm were particularly small (premolt sizes: 92, 96, 99 mm). Consequently, these animals would not be expected to have particularly small increments. Their times at liberty were 325, 187, and 157 days, respectively. We assume that the 93 animals with increments of 6 mm or more molted at least once, and none of the other animals molted. The average time at liberty for animals which did not molt is under a year ($\bar{x}$ 322 days, median 251 days, range 6–1598 days; Fig. 3).

The size at recapture of Conception Bay crabs which molted was plotted against the size at tagging, and two distinct linear clouds of points were apparent (Fig. 4). The line indicating a 17% increase in size appears to separate the two clouds nicely. A reasonable working hypothesis is that the lower cloud consists of animals which molted once, while the upper cloud consists of animals which molted twice. One animal in the two-molt group was at liberty for only 29 days and was tagged and recaptured in a hard-shelled condition. Animals remain soft-shelled for 2–3 months after molting, and soft-shelled animals cannot molt (Taylor et al. 1989).

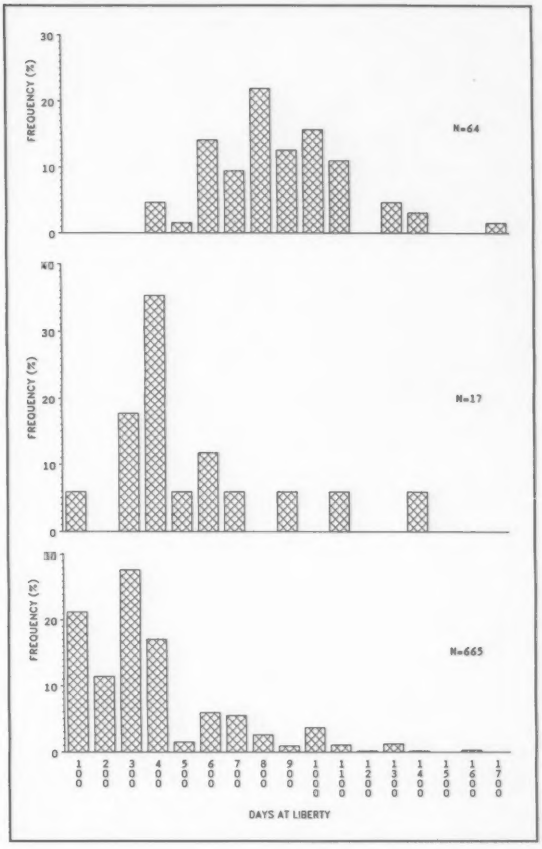

Figure 3

Histograms of times at liberty for Conception Bay *Chionoecetes opilio*. Upper figure corresponds to the upper cloud of points in Figure 4, i.e., to animals believed to have molted twice. Middle figure corresponds to the lower cloud in Figure 4. Lower figure corresponds to recaptured animals which had not molted while at liberty.

For this reason, this animal was eliminated from further consideration.

The times at liberty for 81 of the 92 Conception Bay animals which molted ranged from 18 to 1618 days. (Exact times at liberty could not be determined for 11 animals.) However, the mean time at liberty for the hypothesized two-molter group was approximately twice as long as for the single-molter group (828 vs. 468 days) and there was little overlap in the distributions of time at liberty for the two groups (Fig. 3). Animals which did not molt were at liberty for an average of 322 days. Although there is little information in the literature on intermolt periods for snow crabs, it is believed that crabs approaching commercial size molt once per year (Robichaud et al. 1989) and

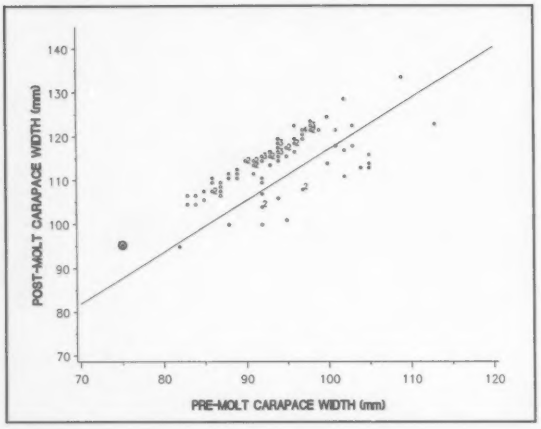

Figure 4

Plot of size at recapture vs. size at tagging for recaptures of *Chionoecetes opilio* from Conception Bay. The solid line, which indicates a 17% increase in size while at liberty, seems to separate the data into two clouds of points. Solid symbols represent animals believed to have molted once; open symbols represent animals which molted twice. Bulls-eye symbol represents one animal which was reportedly at liberty for only 29 days and which consequently was excluded from analysis.

Table 1

Regressions of length at recapture vs. length at tagging for the two groups of *Chionoecetes opilio* from Conception Bay shown in Figure 4. Lower cloud animals are presumed to have molted once; upper cloud, twice. Parameter estimates a and b pertain to equations (1) and (2) in the text.

Attribute	Lower cloud	Upper cloud
Number of observations	20	72
Adjusted r^2	0.85	0.92
Intercept (standard error)	17.250 (8.935)	12.667 (3.640)
Slope (standard error)	0.941 (0.091)	1.104 (0.039)
Interpretation of intercept	a	$a(1+b)$
Interpretation of slope	b	b^2
a	17.250	6.179
b	0.941	1.051

that the largest crabs may skip a year between molts. Thus, the information on time at liberty supports the hypothesis that animals in the lower group of Figure 4 molted once while those in the upper group molted twice.

The data in the lower group in Figure 4 appear to be well described by a linear relationship:

$$\text{Recapture size} = a + b\,(\text{size at tagging}) + e \quad (1)$$

where e is a random error term. Suppose that equation (1) describes the size after one molt. Then the size after two molts would be given by the recursive formula (Kurata 1962):

$$\text{Size after two molts} = a + b\,(a + b\,(\text{size at tagging})) + e. \quad (2)$$

Application of equation (2) to the size at tagging should provide a good prediction of the size at recapture for animals in the upper group if the assumption is correct that equation (1) describes the size after one molt.

We fitted lines to the two clouds of points in Figure 4 by ordinary least squares (Table 1). The results are consistent with the hypothesis of one and two molts for the two groups. For example, the fitted equation (1) (with parameters estimated from the lower cloud of points) predicts that an animal 80 mm in size will be 92.53 mm after one molt. Inserting this estimate of 92.53 mm into equation (1) gives a predicted size of 104.32 mm after another molt. In contrast, a linear regression fitted to the upper cloud of points predicts that an animal 80 mm in size will be 100.91 mm after two molts, i.e., 3.41 mm smaller than the estimate from equation (1). Similarly, the size after two molts predicted by equation (1) for a 110-mm CW animal is 130.89 mm, whereas the size predicted by the regression for the upper cloud is 134.00 mm, i.e., 3.11 mm larger. Over the range of sizes for which we have data, results from the two equations agree closely. In fact, approximate confidence bands for the size after two molts, as determined from the lower regression line, enclose the confidence bands for the upper regression line over the entire range of the data (Fig. 5; see Appendix A for derivation of approximate confidence bands). We therefore conclude that animals in the lower cloud of points molted once, while those in the upper cloud molted twice.

The regressions in Table 1 are based on 20 and 72 animals. Since the sample sizes are small, it would be useful to use the combined molting data from all 92 animals to derive a best estimate of the parameters a and b. This can be accomplished by combining equations (1) and (2) into a single equation in the form of a nonlinear regression model. Let Y be the observed size at the time of recovery, X be the size at tagging, and let Z be an indicator variable for whether an animal molted once or twice, i.e., let

$$Z = \begin{cases} 0, \text{ animal molted once} \\ 1, \text{ animal molted twice.} \end{cases}$$

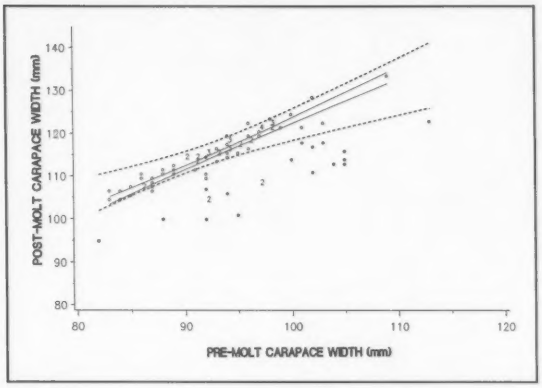

Figure 5

Recapture data for *Chionoecetes opilio* from Conception Bay. Solid symbols represent animals presumed to have molted once; open symbols represent animals which molted twice. Solid lines show the 95% confidence band obtained from the linear regression fitted to the open circle data. Dashed lines give an approximate 95% confidence band for the size after two molts based on the regression for the presumed single-molters (solid symbols). (See Appendix A for method of constructing the confidence band.) The dashed lines enclose the solid lines, indicating that the two predictions of size after two molts are not significantly different. This supports the idea that the two clouds in Figure 3 represent single- and double-molters.

Table 2

Estimates of the parameters a and b in the nonlinear regression model relating size at recapture (Y) of Conception Bay *Chionoecetes opilio* to size at tagging (X) for animals molting once or twice. The model is: $Y = a + abZ + bX + b(b - 1)ZX + e$, where e is the error term and $Z = 0$ if the animal molted once, and 1 if the animal molted twice.

Parameter	Estimate	Standard error	
a	7.398	2.074	correlation
b	1.038	0.021	−0.998

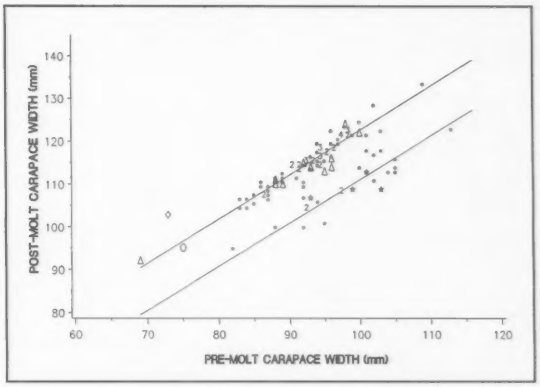

Figure 6

Plot of size at recapture vs. size at tagging for recaptures of *Chionoecetes opilio* from Conception Bay (circles) and Bonavista Bay (triangles and stars). Solid circles and stars represent animals believed to have molted once; open triangles and circles represent animals which molted twice. Diamond represents an animal from Bonavista Bay at liberty for ~1000 days which was presumed to have molted three or more times. Large circle represents an animal which normally would be assumed to have molted twice; however, it was reportedly at liberty for only 29 days and consequently was excluded from analysis. Regression lines were determined using equation (3) from all data on single and double molters from both bays.

Then the growth parameters a and b can be estimated by regressing Y on X and Z in the regression model

$$Y = a + abZ + bX + b(b - 1)ZX + e \qquad (3)$$

where e is a random error term. Equation (3) reduces to (1) when $Z = 0$ and to (2) when $Z = 1$. The model is generalized in Appendix B to account for a quadratic relationship between post- and pre-molt size. The predicted sizes from the fitted equation (3) (Table 2) are very similar to the results obtained using equations (1) and (2) separately.

Bonavista Bay

Molt information was obtained from 18 animals recaptured in Bonavista Bay. Of these, four animals appeared to have molted once; 13 animals appeared to have molted twice; and one animal at liberty for approximately 1000 days appeared to have molted three or more times (Fig. 6). This interpretation is supported by the fact that the animals presumed to have molted once were at liberty for an average of 198 days, while the animals presumed to have molted twice were at liberty for an average of 698 days.

The molt increments appeared very similar to those from Conception Bay. Since there is not much information from Bonavista Bay, we computed a regression to predict molt increments for Bonavista Bay crabs using the combined recapture data on single and double molters from Bonavista and Conception Bays. The predicted size after molting is given by

$$\text{Predicted size} = 9.21 + 1.02\ (\text{pre-molt size}).$$

Other populations

The predicted molt increments from equation (3) for Conception Bay crabs (Table 2) were very close to a constant (10.5 – 11.7 mm) over the size range of animals we studied (82–113 mm CW). These estimates are

consistent with the limited information from a tagging study in the Gulf of Alaska. McBride (1982) reported the mean growth increment of six tagged snow crabs at liberty for up to 1 year was 14.7 mm. McBride's animals were somewhat larger than those in our study ($\bar{x}$ 113.8 mm, range 108–124 mm CW at tagging) and would, on the basis of our regression, be predicted to have slightly larger molt increments.

Laboratory studies of snow crab growth are also consistent with our findings. O'Halloran (1985) reported an average molt increment of 11.6 mm for eight animals. However, five of the eight animals had their eyestalks ablated bilaterally and these animals died during ecdysis. Consequently, these estimates are not very reliable. Miller and Watson (1976) and R.J. Miller (Dep. Fish. Oceans, Halifax, Nova Scotia, Canada 83J 2S7, pers. commun., June 1989) observed a mean molt increment of 15.5 mm for 18 crabs ranging in pre-molt size from 59.3 to 101.1 mm CW ($\bar{x}$ 80.5 mm). G. Hurley (Hurley Fish. Consulting, 45 Alderney Dr., Dartmouth, Nova Scotia, Canada B2Y 2N6, pers. commun., June 1989) observed a mean increment of 13.9 mm for 47 crabs, size range 60.7–83.4 mm CW ($\bar{x}$ 66.1 mm). In these studies, crabs were fed *ad libitum*. In another laboratory study, Moriyasu et al. (1987) reported a regression line that indicates that animals in the size range we studied (82–113 mm CW) have predicted molt increments of 14–16 mm CW.

Molt increments have also been estimated by size-frequency analysis for Japanese populations of snow crabs. Kon et al. (1968) reported estimates for small individuals. Ito (1970) suggested that 81-mm CW individuals molt to 97 mm, then to 111 mm and 121 mm (i.e., molt increments of 16, 14, and 10 mm). Kon (1980) suggested that 80-mm CW individuals molt to 93.4 mm, then to 105.6 and 116.7 mm (molt increments of 13.4, 12.2, and 11.1 mm). These estimates are similar to the ones we derived from the tagging data. Robichaud et al. (1989) analyzed size-frequency distributions of snow crabs from the Gulf of St. Lawrence. Their samples consisted of small animals, so their results are not comparable to the results presented here.

Effect of possible terminal molt

Some workers believe that male snow crabs undergo a "terminal" or final molt which is associated with a change in allometry. Although this idea is controversial (see Jamieson and McKone 1988 for reviews), it is worth examining whether the two groups evident in Figure 4 might reasonably be interpreted as those molting to the terminal state (e.g., lower group) and those molting but not to the terminal state (upper group). To accept this hypothesis implies that all of the following are accepted:

(1) males do, in fact, undergo a terminal molt;

(2) the size increment at the terminal molt is considerably different (presumably smaller) than the penultimate molt increment;

(3) it is a coincidence that the animals in the upper group were at liberty twice as long as those in the lower group (828 vs. 468 days on average), and that the animals which did not molt were at liberty for less than a year on average ($\bar{x}$ 322 days);

(4) it is a coincidence that the size predicted after two molts by the regression fitted to the lower cloud of points is in close agreement to the size after two molts predicted by the regression fitted to the upper cloud of points;

(5) there must be an as yet unidentified reason why a third cloud of points, corresponding to animals which molted twice, is not evident in Figure 4.

Even if males undergo a terminal molt, there is no evidence to suggest that the final molt increment is distinctly smaller than the penultimate molt increment. In an aquarium study, Moriyasu et al. (1987) found, for male snow crabs in the size range 60–70 mm CW, that animals molting to the large-clawed state have molt increments about 3 mm smaller than those molting to a small-clawed state. This small difference in molt increments is not sufficient to account for the two clouds we identified in the field observations. Ennis et al. (1988) have shown that males can become functionally mature before attaining the morphometry associated with the terminal molt. Hence, the terminal molt is not necessarily associated with a diversion of energy from growth to reproductive processes, and the terminal molt increment need not be small. We conclude that if animals undergo a terminal molt, the molt increment at this time is similar to the penultimate molt increment. We do not rule out the possibility that some of the scatter about the regressions through the two clouds of points is due to mixing terminal and non-terminal molt data.

In summary, our interpretation of the tagging data is supported by two lines of evidence. Animals presumed to have molted twice were at liberty twice as long on average as animals presumed to have molted once. Also, the predicted size after two molts, as estimated from data on animals presumed to have molted once, agrees closely with the predicted size estimated from data on animals presumed to have molted twice. We conclude that male snow crabs in the size range 75–115 mm have molt increments of around 11 mm. Our results are consistent with the limited information about snow crab growth in the literature.

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Citations

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Appendix A
Derivation of Confidence Bands

The predicted size after one molt can be obtained by regressing the size at recapture on the size at tagging for those animals which molted once (text equation 1). Thus,

$$\text{predicted recapture size} = a + bX \qquad (A.1)$$

where a and b are parameter estimates and X is the size at tagging. Estimates of the variances and covariances (i.e., $V(a)$, $V(b)$, $Cov(a,b)$) are easily obtained in the standard way.

The predicted size after two molts is obtained from A.1 as

$$Y = \text{predicted size after two months}$$
$$= a + b(a + bX) = a + ab + b^2X.$$

An approximate (asymptotic) estimate of the variance of the size after two months, V(Y), is found by the Taylor's series or delta method to be

$$V(Y) = \left(\frac{\partial Y}{\partial a}\right)^2 V(a) + \left(\frac{\partial Y}{\partial b}\right)^2 V(b)$$
$$+ 2\left(\frac{\partial Y}{\partial a}\right)\left(\frac{\partial Y}{\partial b}\right) Cov(a,b)$$

where the derivatives are evaluated at the parameter estimates. Thus.

$$V(Y) = (1 + b)^2 V(a) + (a + 2bx)^2 V(b)$$
$$2(1 + b)(a + 2bx)\, Cov(a,b).$$

An approximate 95% confidence band is thus obtained as

$$Y \pm 2\sqrt{V(Y)}.$$

Appendix B Estimating molt increments for a quadratic model

Over the size range of animals we studied, the relationship between post- and pre-molt size appeared linear. However, when a wide range of pre-molt sizes is considered, it is common to find a curvilinear relationship which may be modeled satisfactorily by a quadratic equation. The non-linear regression model (equation 3) in the text can be generalized to allow estimation for the quadratic model.

Let the size at tagging be denoted by X, and assume the size after one molt is given by

$$\text{size after one molt} = a + bX + cX^2. \qquad (B.1)$$

Then the size after two molts is given by

$$\text{size after 2 molts} = a + b(a + bX + cX^2)$$
$$+ c(a + bX + cX^2)^2. \qquad (B.2)$$

As before, let Y be the size at recapture (for animals molting once or twice), and define Z to be an indicator variable for whether an animal molted once or twice, i.e., let

$$Z = \begin{cases} 0, \text{ animal molted once} \\ 1, \text{ animal molted twice} \end{cases}$$

Then equations (B.1) and (B.2) can be combined in a single non-linear regression as

$$Y = a + (ab + a^2c)Z + bX + b(b - 1 + 2ac)ZX$$
$$+ c^2X + c(b + 2ac + b^2 - 1)ZX^2$$
$$+ 2bc^2ZX^3 + c^3ZX^4 + e \qquad (B.3)$$

where e is the random error term. Equation (B.3) reduces to (B.1) when Z = 0 and to (B.2) when Z = 1.

A Practical Assessment of the Performance of Shepherd's Length Composition Analysis (SRLCA): Application to Gulf of Maine Northern Shrimp *Pandalus borealis* Survey Data

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Abstract.– We applied Shepherd's length composition analysis (SRLCA) to research trawl survey catches of Gulf of Maine northern shrimp *Pandalus borealis* to test the efficiency of the method in interpreting the age structure of a length-frequency distribution incorporating significant variation in growth and recruitment rates. We evaluated the performance of the method by comparing the von Bertalanffy growth parameters provided by SRLCA and subsequently derived age frequencies and instantaneous total mortality rates with previously accepted results based on simple visual inspection of the annual length-frequency distributions.

In spite of the variable growth and recruitment rates exhibited by the stock, SRLCA yielded information providing a resolution of the length-frequency data close to *a priori* assumptions, although information external to the procedure was needed to select the best interpretation from among several locally optimal solutions.

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The analysis of length-frequency modes was the first method used by aquatic biologists to delineate successive cohorts in fish and invertebrate populations. Simple visual inspection of modes was developed first (e.g., the "Petersen" method [Petersen 1891]); this relies heavily on the intuition of the scientist for the correct separation of age groups. Later workers assumed a normal distribution underlying the observed length modes, and graphical methods using normal probability paper were used to resolve length distributions to cohorts by the successive identification and removal of suspected age groups. The method of Cassie (1954) is probably the best known of these graphical procedures, which rely to a large degree on subjective decisions of the scientist. Difficulty in defining modes for older age groups, problems in interpretation caused by variable growth rates and recruitment, and an inability to reproduce the interpretation of age groups from one worker to the next have limited the utility of these simple methods.

For most finfish stocks, the interpretation of growth intervals on hard body parts (e.g., scales, otoliths, spines, and vertebrae) has evolved as the ageing method of choice, replacing length-composition analysis methods. For many taxa, however, the interpretation of growth intervals from age structures is difficult, either due to problems in identifying periodic marks or because of the lack of suitable hard structure. For fast-growing, short-lived tropical finfish, and invertebrates such as lobsters, crabs, shrimps, and squids, the resolution to ages of modes in length-frequency distributions continues to be the primary method used to estimate growth and age structure of populations. Recently developed methods directed to interpreting length-frequency distributions generally fall into two categories. The first group treats the problem as one of statistically resolving a mixture of distributions, and usually assumes an underlying normal distribution for the components. The parameters resulting in the best match between the area under the theoretical distribution and the area under the observed length distribution are selected by employing chi-square or maximum likelihood methods. These distribution mixture methods require some prior constraint on the number of length modes and the bounds of the parameters to prevent biologically unrealistic results. The lineage of this approach includes the methods of Hasselblad (1966), Tomlinson (computer program

NORMSEP; 1971), Yong and Skillman (computer program ENORMSEP; 1975), McNew and Summerfelt (1978), and MacDonald and Pitcher (computer program MIX; 1979). The distribution mixture method of Schnute and Fournier (1980) uses a growth model to impose these constraints. A second category of procedures assumes a specific growth function (usually the von Bertalanffy) and attempts to match predicted length modes to those observed. Among these methods are the ELEFAN I procedure of Pauly and David (1981), and Shepherd's length composition analysis (1987).

The Shepherd length composition analysis method (SRLCA) (Shepherd 1987) relies on a goodness-of-fit score function which varies according to the correspondence of observed and predicted length-frequency modes for given pairs of von Bertalanffy growth parameters (L_{inf} and K), thus presumably constraining the indication of optimal parameters to within biologically realistic bounds. SRLCA has fewer subjective input requirements than the distribution mixture methods (Shepherd 1987). Basson et al. (1988) performed Monte Carlo tests of SRLCA and noted that although SRLCA provided biased results for simulated data with large variation in length-at-age, SRLCA generally performed better than ELEFAN I.

To test the performance of SRLCA on an observed, potentially difficult-to-interpret data set, as suggested by Shepherd (1987), we applied a version of SRLCA using the von Bertalanffy growth equation to research trawl survey data for Gulf of Maine northern shrimp *Pandalus borealis*, and compared our results with accepted interpretations of the data. Currently, simple visual inspection and information on sexual characteristics are used to resolve survey length frequency to age frequency, providing subsequent estimates of relative adult stock abundance, recruitment success, and total instantaneous mortality rates (Z) (McInnes 1986, NSTC 1987). Survey results reveal that this stock has experienced variable recruitment and growth during 1982 to 1988 (NSTC 1984, 1985, 1986, 1987, 1988). Although true ages for northern shrimp are not available for use as "ground truth" in this evaluation of SRLCA performance, we feel our assessment of the method is valuable since it is based on application to real data of the type which in practice might require the use of length-based assessment methodology.

Methods

Analysis

SRLCA compares the observed length-frequency distribution with that expected from the von Bertalanffy equation for given test pairs of L_{inf} and K by application of a continuous, periodic test function of the form:

$$T_i = ([\sin \pi \{t_{max} - t_{min}\}] / [\pi \{t_{max} - t_{min}\}]) \times (\cos 2\pi [t_{bar} - t_s])$$

where T_i is the value of the function for a given length interval i, t_{max} and t_{min} are ages at the upper and lower bounds of the interval for a given test set of growth parameters, t_{bar} is the average of t_{max} and t_{min}, and t_s is the date of observation, expressed as a fractional part of the age (e.g, annual) cycle (Shepherd 1987).

A measure of goodness-of-fit is then used to determine the best fitting set of growth parameters for the observed length-frequency distribution. This measure, the score function S, is given by:

$$S = \sum_i T_i N_i^{1/2}$$

where i indexes the length intervals, T is as indicated previously, and N is the number of animals in each interval. Taking the square root of N helps reduce the sensitivity of the score function to unusually large numbers of animals in a given length interval (e.g., in the event of exceptional recruitment; Shepherd 1987). Cumulative scores are large and positive when length modes predicted for a given pair of growth parameters are consistent with observed length-frequency modes, with negative scores indicating inconsistency. Shepherd (1987) suggested that regions of nearly constant scores within the K by L_{inf} score matrix may provide an indication of the shape of the confidence interval around pairs of parameters (e.g., Shepherd suggests a region equal to one-half of the maximum score might approximate the 95% confidence interval). Typically, several regions (hereafter called ridges) of high scores will be observed for each length-frequency distribution analyzed, with local maxima in each ridge that provide alternative interpretations of the data.

Length-frequency data

Gulf of Maine northern shrimp are protandric hermaphrodites, with the females the target of a valuable winter/spring fishery in the western Gulf of Maine (see McInnes 1986 for an overview of the fishery). A research vessel trawl survey was implemented in 1983 to provide a fisheries-independent source of data for the stock. A stratified random trawl survey is conducted annually during late July through mid-August aboard the Northeast Fisheries Center (NEFC) RV *Gloria Michelle* in the western Gulf of Maine (Fig. 1).

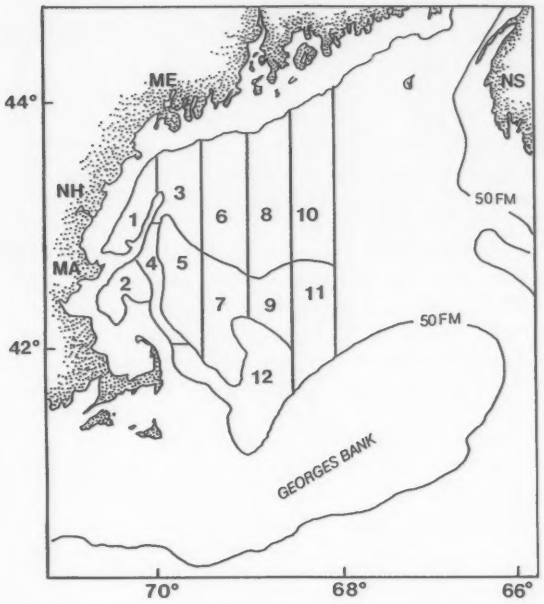

Figure 1

Western Gulf of Maine region with major bathymetric features and 50-fathom (100-m) isobath. Northern shrimp survey area extends from 68°W longitude to the 50-fathom isobath, except for stratum 2, where the sampled area extends to the 30-fathom (60-m) isobath.

Length-frequency data from identical sample strata sets (strata 1, 3, and 5–8) are available for 1984–88 (NSTC 1984, 1985, 1986, 1987, 1988). Trawl gear consists of a modified 4-seam commercial shrimp trawl with 35 mm (1.4 inch) stretched mesh in the body of the net and 32 mm (1.3 inch) stretched mesh in the extension and codend, with "rockhopper" ground gear to allow sampling over rough bottom (McInnes 1986). Samples (2 kg) of each tow are retained for length measurement and sex determination. All shrimp in the sample are measured, with mid-dorsal carapace lengths aggregated by 0.5-mm intervals (nearest 0.5 mm below that measured). A 1-kg subsample is retained for determination of sex and spawning stage.

To date, abundance and biomass indices from the RV *Gloria Michelle* survey (stratified mean number per tow, stratified mean weight [kg] per tow) have proven to be accurate predictors of year-class size and commercial fishery performance (total catch and catch-per-unit-effort; NSTC 1988). Coefficients of variation for stratified mean number and weight (kg) per tow, aggregated over all sample strata, have averaged (1984–88) about 13% and 12%, respectively, indicating relatively high precision.

A priori assumptions

Information is available from previous analyses of the Gulf of Maine northern shrimp length-frequency distributions to provide a baseline interpretation for evaluation of SRLCA results. The von Bertalanffy growth equation has been the accepted means of describing the growth of *P. borealis* (Frechette and Parsons 1983). For the Gulf of Maine stock, growth parameters were expected to be in the range of those previously estimated for this stock. These include (1) parameters derived here by nonlinear least-squares regression analysis of mean carapace length (CL) at age data summarized by Haynes and Wigley (1969; L_{inf} = 32 mm, K = 0.46, t_0 = −0.12), and (2) parameters derived from NEFC groundfish bottomtrawl survey data for northern shrimp (NEFC unpubl. data in McInnes 1986; L_{inf} = 35.2 mm, K = 0.36, t_0 = 0.06). In both of these studies, age was estimated by visual inspection of length-frequency distributions.

For Gulf of Maine northern shrimp survey data, a 1 March birthday was assumed (Apollonio et al. 1986), with an average catch date of 1 August (NSTC 1984, 1985, 1986, 1987, 1988); thus t_s was set equal to 0.42 for all SRLCA runs in this exercise. The usual presence of four age groups (ages 1–4) in the survey catch was suspected (McInnes 1986), with a maximum age of 5 years (Haynes and Wigley 1969, Apollonio et al. 1986), based on modes in length frequencies and sexual characteristics (Allen 1959, McCrary 1971). Northern shrimp in a length range of 13–18 mm CL are generally assumed to be of age-group 1, and mainly immature and mature males, while shrimp 18–22 mm CL are assumed to be age 2 and mostly mature males. Animals in the 22–25 mm CL interval are assumed age 3, usually females with no previous spawning history. Shrimp larger than 25 mm CL are assumed to be females of age-group 4, with possible age-group 5 female shrimp at CL greater than 29 mm. The survey samples northern shrimp in a CL range of 10–32 mm (Fig. 2), with animals assumed fully recruited to the gear at about 19–20 mm CL, or age 2 and older (Blott et al. 1983). Previous interpretations of survey results and commercial fishery performance suggest that the 1982 and 1987 year-classes (YC) of Gulf of Maine northern shrimp were strong, and the 1983 YC very weak, with the remaining cohorts (1984–86) of about equal strength (NSTC 1987, 1988).

Model evaluation

Exploratory runs were performed using L_{inf} values ranging from 20 to 50 mm, in 1-mm steps, and K values ranging from 0.20 to 0.50, in 0.01 steps, encompassing a very wide range of values (about ±50%) around

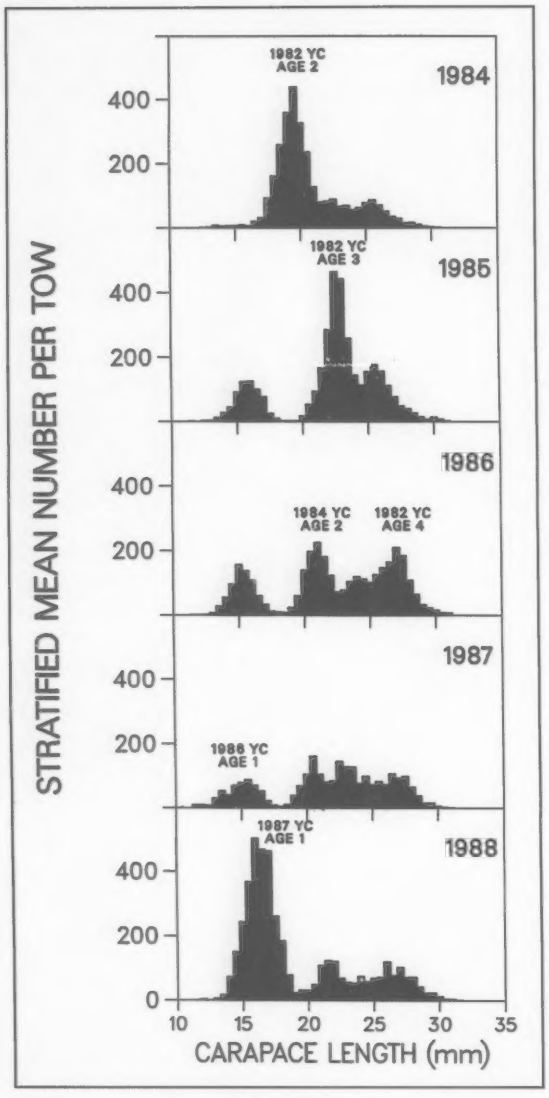

Figure 2

Length-frequency distributions (stratified mean number per tow) for *Pandalus borealis* collected in the western Gulf of Maine during the 1984–88 northern shrimp surveys aboard RV *Gloria Michelle*.

the growth parameters previously estimated for this stock of *P. borealis*, in order to adequately explore the high score ridges provided by the SRLCA score function. Preliminary evaluation of the highest scoring parameter values from each ridge, along with several local maxima (higher score than all eight nearest neighbors) within each ridge, indicated that parameter pairs within a given ridge tended to provide similar interpretations of the number of modes (assumed age groups) present in the observed length frequency, as expected from earlier testing of the method (Shepherd et al. 1987). Values of the optimum value of t_0 corresponding to K and L_{inf} parameter pairs are the decimal fraction part of t_0, and are indeterminate with respect to the addition or subtraction of any whole number of years (Shepherd 1987).

SRLCA results were examined in the context of previously developed parameter estimates and *a priori* assumptions, and alternative parameters were evaluated when the highest scoring values did not agree with prior interpretations of the number and position of modes (assumed age groups) expected. SRLCA was first applied to annual distributions independently, and then to distributions from 1984 to 1988 sequentially pooled in a single run. The annual distributions were analyzed primarily to evaluate interpretations provided by SRLCA given the variable patterns of growth and recruitment in the data. Growth parameters and subsequently resolved age frequencies from the final pooled analysis were used to estimate total mortality for comparison with rates estimated by visual resolution of the length-frequency data to age.

Shepherd (1987) noted that the number of older ages determined by decomposition of the length-frequency distribution according to the von Bertalanffy growth equation is dependent to a large degree on the value of L_{inf}, and suggested that parameters selected by SRLCA might be most appropriate for subsequent use in other length-based analyses, rather than to slice length frequencies to ages, unless additional data (e.g., knowledge of the expected number of cohorts) are available to select the ridge containing the "correct" parameter pair (see also Shepherd et al. 1987). In this exercise, we elected to proceed with resolution to cohorts, and subsequent age-based mortality estimation, both because of the apparently nonequilibrium nature of this northern shrimp population (thus limiting the utility of length-based methods which assume steady-state conditions), and to provide results comparable with those previously estimated (NSTC 1984, 1985, 1986, 1987, 1988).

Results

Annual length frequencies

1984 distribution This distribution is characterized by a dominant mode centered at 19.5 mm (Fig. 2). *A priori* interpretation suggested that the dominant mode at 19–20 mm should be age-group 2 shrimp (a strong 1982 YC), with shrimp 22–24 mm probably age-

Table 1

Von Bertalanffy growth parameter pairs and SRLCA score (S) for 1984 northern shrimp survey length-frequency distribution: primary and secondary ridge crests.

	L_{inf} (mm)	K	S
Primary ridge crest	35	0.50	47.0
	40	0.43	63.9
	45	0.36	64.4
	50	0.30	62.7
	39	0.50	67.7[1]
	41	0.43	65.8[2]
Secondary ridge crest	35	0.42	41.4[1]
	40	0.30	37.4
	36	0.37	40.3[2]*

[1] High score parameters of ridge crest, on boundary of explored space.
[2] High score parameters of ridge crest, nonboundary maximum.
* Parameters selected for final evaluation.

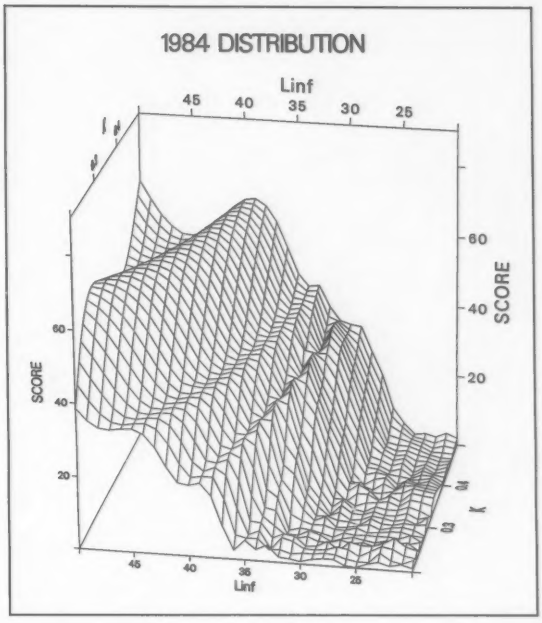

Figure 3

Response surface of the SRLCA score function for the northern shrimp survey 1984 length-frequency distribution.

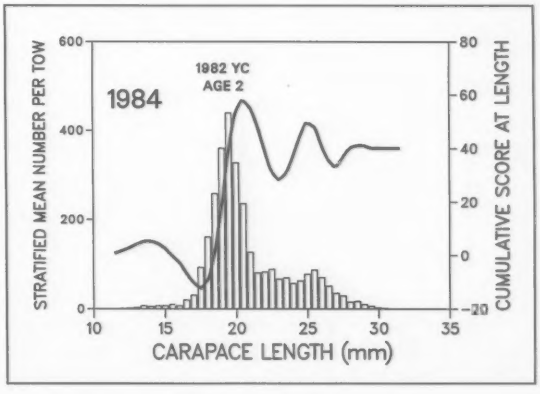

Figure 4

Northern shrimp survey 1984 length-frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (L_{inf} = 36 mm, K = 0.37).

group 3, and animals >25 mm defined as age 4+ (NSTC 1984). SRLCA scores exhibited a broad, primary (highest scores) ridge of scores within the explored parameter space ranging from a high score on the border of explored parameter space at L_{inf} = 39 mm, K = 0.50 to L_{inf} = 50 mm, K = 0.30, with a nonboundary local maximum at L_{inf} = 41 mm, K = 0.43 (Table 1, Fig. 3). Based on parameters in this ridge, the length frequency was interpreted as a single dominant mode (age-group 1), with the distribution to the right of the mode classified as two older age-groups, for a total of three cohorts present. A secondary ridge of scores, from L_{inf} = 33 mm, K = 0.50 to L_{inf} = 38 mm, K = 0.30, with a nonboundary local maximum at L_{inf} = 36 mm, K = 0.37 (Table 1, Fig. 3), classified four ages and defined the dominant mode as age 2, but did not interpret the small modes at 22.5 and 25.5 mm in accordance with prior assumptions (assumed age groups 3 and 4, respectively). However, this secondary ridge most closely matched the *a priori* interpretation, and represented the best performance of SRLCA for the 1984 data (Fig. 4). A tertiary ridge (a spur of the secondary) ranged from a nonboundary maximum at L_{inf} = 31 mm, K = 0.46 to L_{inf} = 34 mm, K = 0.30, and interpreted the length frequency in nearly the same manner as parameters from the secondary ridge.

1985 distribution Previous work suggested that the first two modes of this distribution, 13–18 mm and 20–24 mm, should be interpreted as age groups 1 (1984 YC) and 3 (the strong 1982 YC), thus confronting SRLCA with a "missing cohort" situation (the weak 1983 YC; Fig. 2). Sex determinations further showed that shrimp in the 20–24 mm mode were not the expected first-year females, but mostly mature males that seemed not to have undergone t ..nsition during the previous winter (NSTC 1985). Inspection of the position of this age-3 mode, relative to the modal lengths

Table 2
Von Bertalanffy growth parameter pairs and SRLCA score (S) for 1985 northern shrimp survey length-frequency distribution: primary, secondary, and tertiary ridge crests.

	L_{inf} (mm)	K	S
Primary ridge crest	35	0.48	85.2[2]
	40	0.34	82.6
	45	0.26	78.7
	50	0.21	75.2
Secondary ridge crest	42	0.50	63.0
	46	0.41	69.7
	50	0.34	74.1[1]
Tertiary ridge crest	28	0.50	29.0[1]
	30	0.37	23.6
	32	0.30	22.5
	34	0.27	21.4
	36	0.23	23.4
	38	0.20	23.8
	29	0.42	25.3[2]*

[1] High score parameters of ridge crest, on boundary of explored space.
[2] High score parameters of ridge crest, nonboundary maximum.
*Parameters selected for final evaluation.

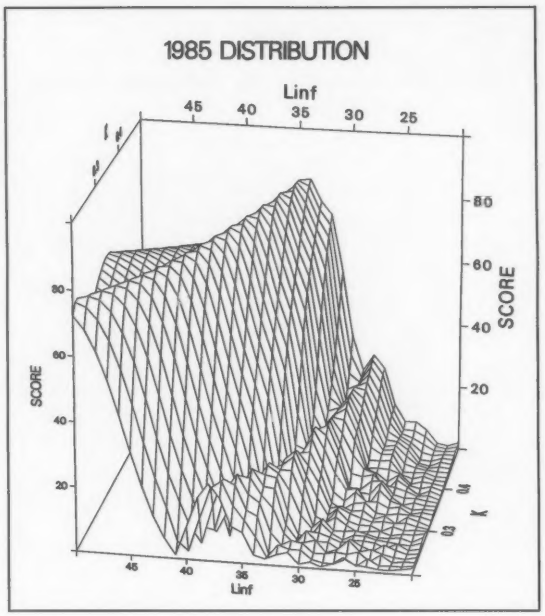

Figure 5
Response surface of the SRLCA score function for the northern shrimp survey 1985 length-frequency distribution.

of assumed age-3 shrimp in the two subsequent years, suggests that the 1982 YC may also have experienced a slower growth rate between ages 2 and 3 than preceding cohorts.

The highest value in the SRLCA primary score ridge was at L_{inf} = 35 mm, K = 0.48, with the ridge then continuing to L_{inf} = 50 mm, K = 0.21. Parameters in this primary ridge classified the first two modes as successive cohorts, with three age groups total. A secondary ridge, from L_{inf} = 42 mm, K = 0.50 to a boundary maximum at L_{inf} = 50 mm, K = 0.34, resolved the distribution to only two age groups, with modal lengths of 17.0 and 26.5 mm for ages 1 and 2. It was necessary to explore a tertiary ridge, with a nonboundary local maximum at L_{inf} = 29 mm, K = 0.42, to successfully interpret the first two length modes as age groups 1 and 3, with shrimp >24.5 mm resolved to two main age-groups (Table 2; Fig. 5, 6).

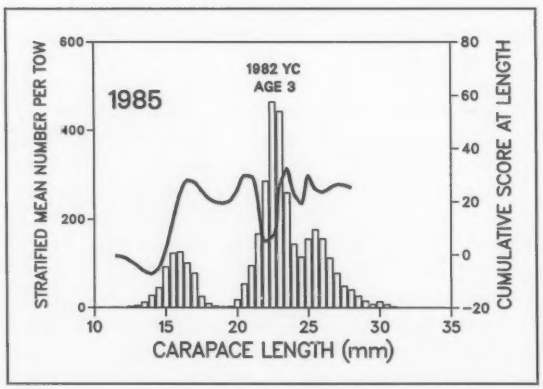

Figure 6
Northern shrimp survey 1985 length-frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (L_{inf} = 29 mm, K = 0.42).

1986 distribution This distribution is characterized by three clearly defined modes at 13–18 mm, 19–22 mm, and >25 mm, assumed to be ages 1, 2, and 4, and a small mode at 23 mm assumed to be either the 1983 cohort at age 3 or slow-growing shrimp from the 1982 cohort at age 4 (NSTC 1986; Fig. 2). Two ridges of comparable high scores were apparent from an initial SRLCA run, a primary ridge from L_{inf} = 35 mm, K = 0.49 to a boundary maximum at L_{inf} = 50 mm, K = 0.22, and a secondary ridge from L_{inf} = 32 mm, K = 0.47 to L_{inf} = 40 mm, K = 0.23 (Table 3, Fig. 7). The primary ridge identified three modal groups, matching the first observed mode well, but classifying shrimp between 18.5 and 24.5 mm as a single group, with the

Table 3
Von Bertalanffy growth parameter pairs and SRLCA score (S) for 1986 northern shrimp survey length-frequency distribution: primary and secondary ridge crests.

	L_{inf} (mm)	K	S
Primary ridge crest	35	0.49	65.5
	40	0.34	74.1
	45	0.26	78.0
	50	0.22	79.9[1]
Secondary ridge crest	32	0.47	65.1
	34	0.37	65.6
	36	0.31	63.1
	38	0.27	59.9
	40	0.23	55.7
	33	0.42	66.1[2]*

[1] High score parameters of ridge crest, on boundary of explored space.
[2] High score parameters of ridge crest, nonboundary maximum.
*Parameters selected for final evaluation.

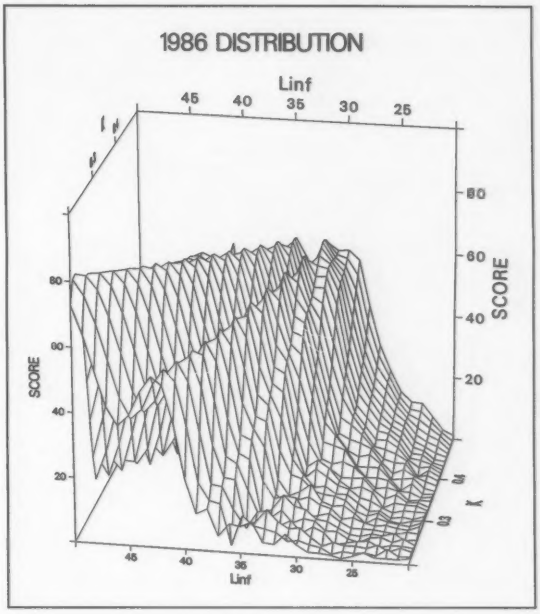

Figure 7
Response surface of the SRLCA score function for the northern shrimp survey 1986 length-frequency distribution.

last mode interpreted as age-3 shrimp. The secondary ridge high-score parameters classified the first, second, and fourth observed modes fairly well, with the highest scoring parameters (L_{inf} = 33 mm, K = 0.42) falling in an interval between previously estimated von Bertalanffy parameters. SRLCA was thus able to match the *a priori* interpretation of the 1986 length-frequency distribution reasonably well, using parameters from the secondary ridge crest (Fig. 8).

1987 distribution The first mode of this distribution is fairly pronounced and has been interpreted as age 1, but the modes following are not well defined (NSTC 1987; Fig. 2). SRLCA indicated best fitting parameter pairs in a primary score ridge ranging from L_{inf} = 35 mm, K = 0.50 to L_{inf} = 50 mm, K = 0.23, with a maximum at L_{inf} = 40 mm, K = 0.36, and in a secondary ridge ranging from L_{inf} = 32 mm, K = 0.50 to L_{inf} = 40 mm, K = 0.24, with a nonboundary local maximum at L_{inf} = 33 mm, K = 0.43 (Table 4, Fig. 9). The primary ridge parameters defined three age groups, correctly classifying the first mode, lumping shrimp between 19.0 and 25.0 mm as a second group, and aggregating all shrimp >25 mm as a final group. The secondary ridge parameters resolved the distribution in a similar manner, but by splitting shrimp >23 mm into two groups (Fig. 10). Thus, neither set of parameters selected by SRLCA successfully resolved shrimp between 19.0 and 25.0 mm to distinct cohorts.

1988 distribution In the 1988 survey length frequency, the large mode between 13 and 19 mm was assumed to be age-1 shrimp. A smaller mode of 20–23 mm was interpreted as age 2, with shrimp >25 mm assumed, as usual, to be age-group 4+ (NSTC 1988; Fig. 2). SRLCA provided two ridges of high scoring parameters, a primary ridge extended from a boundary max-

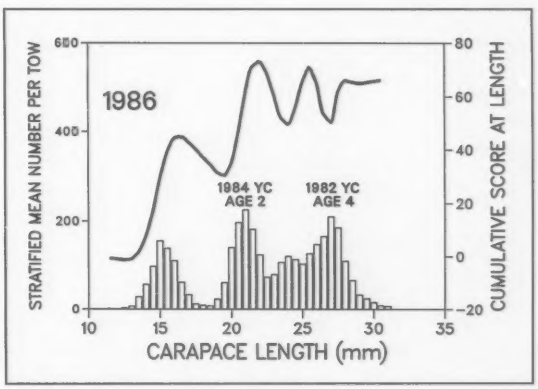

Figure 8
Northern shrimp survey 1986 length-frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (L_{inf} = 33 mm, K = 0.42).

Table 4

Von Bertalanffy growth parameter pairs and SRLCA score (S) for 1987 northern shrimp survey length-frequency distribution: primary and secondary ridge crests.

	L_{inf} (mm)	K	S
Primary ridge crest	35	0.50	55.0
	40	0.36	57.1[2]
	45	0.28	56.7
	50	0.23	55.9
Secondary ridge crest	32	0.50	42.5[1]
	34	0.39	40.1
	36	0.32	37.9
	38	0.28	35.5
	40	0.24	34.0
	33	0.43	41.3[2]*

[1] High score parameters of ridge crest, on boundary of explored space.
[2] High score parameters of ridge crest, nonboundary maximum.
*Parameters selected for final evaluation.

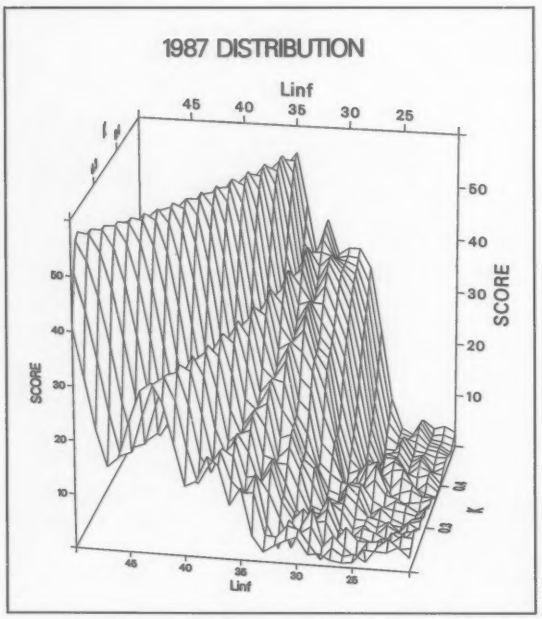

Figure 9

Response surface of the SRLCA score function for the northern shrimp survey 1987 length-frequency distribution.

imum at L_{inf} = 43 mm, K = 0.50 to L_{inf} = 49 mm, K = 0.39, while a secondary ridge ranged from L_{inf} = 35, K = 0.47 to L_{inf} = 50 mm, K = 0.20 (Table 5, Fig. 11).

Values from the primary ridge resolved shrimp 11–21.5 mm as a single cohort (age 1), with animals 22 mm and larger assigned to age 2. Values from the secondary ridge provided only a slightly improved interpretation, with shrimp 11–19.5 mm classified as age 1, 20–25 mm as age 2, and >25 mm as age 3. Clearly, the modes in this distribution were not sufficiently distinct to allow a reasonable interpretation using SRLCA (Fig. 12).

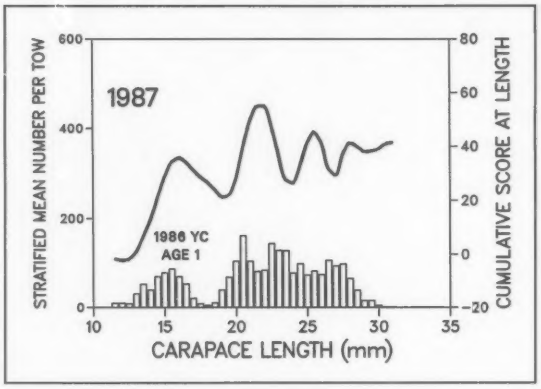

Figure 10

Northern shrimp survey 1987 length-frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (L_{inf} = 33 mm, K = 0.43).

Table 5

Von Bertalanffy growth parameter pairs and SRLCA score (S) for 1988 northern shrimp survey length-frequency distribution: primary and secondary ridge crests.

	L_{inf} (mm)	K	S
Primary ridge crest	43	0.50	123.5[1]
	45	0.46	123.0[2]
	47	0.42	122.4
	49	0.39	121.9
Secondary ridge crest	35	0.47	93.3[2]*
	40	0.34	88.5
	45	0.25	85.0
	50	0.20	85.0

[1] High score parameters of ridge crest, on boundary of explored space.
[2] High score parameters of ridge crest, nonboundary maximum.
*Parameters selected for final evaluation.

Pooled distribution: 1984–88 As with the annual distributions, an exploratory run was made with L_{inf} values ranging from 20–50 mm, in 1-mm steps, and K values of 0.20–0.50, in 0.01 steps. Two broad regions

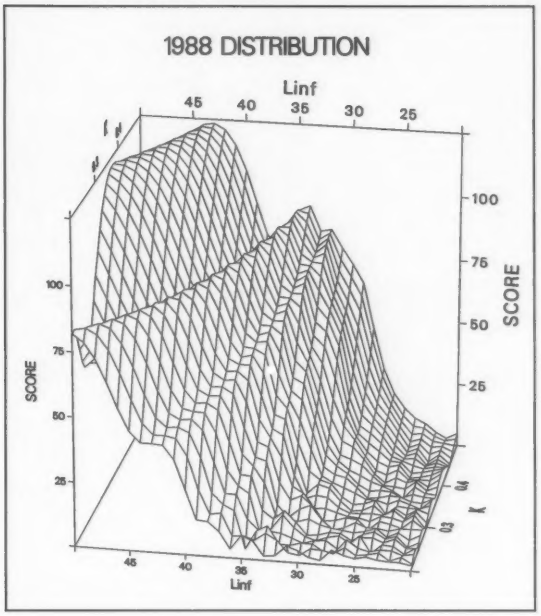

Figure 11
Response surface of the SRLCA score function for the northern shrimp survey 1988 length-frequency distribution.

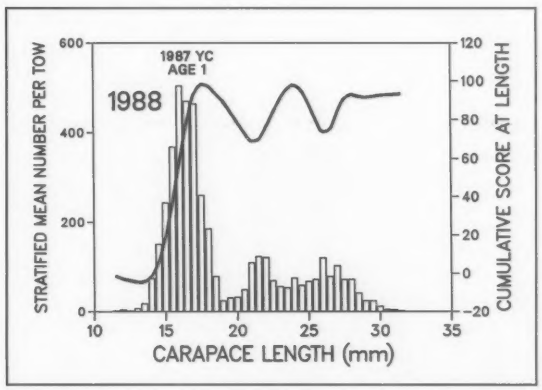

Figure 12
Northern shrimp survey 1988 length-frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (L_{inf} = 35 mm, K = 0.47).

of parameters, with a primary ridge in one region and secondary, tertiary, and quaternary ridges in the other, were evaluated in an attempt to find parameters selected by the SRLCA test function that would interpret the 1984–1988 distributions in accordance with *a priori* assumptions.

Table 6
Von Bertalanffy growth parameter pairs and SRLCA score (S) for pooled 1984–88 northern shrimp survey length-frequency distribution: primary, secondary, tertiary, and quaternary ridge crests.

	L_{inf} (mm)	K	S
Primary ridge crest	43	0.50	244.0
	44	0.47	244.8
	46	0.43	245.7
	48	0.40	246.5[2]
	50	0.37	247.8[1]
Secondary ridge crest	35	0.50	219.2
	35	0.48	227.0
	36	0.44	230.3
	38	0.38	233.7
	40	0.34	234.0
	42	0.30	234.9[2]
	44	0.27	234.2
	46	0.25	233.4
	48	0.23	232.5
	50	0.21	232.1
Tertiary ridge crest	32	0.50	190.0
	32	0.49	191.4[2]
	33	0.43	175.0
	34	0.39	160.0
	35	0.35	147.3
	37	0.29	127.9
	40	0.23	108.9
	43	0.20	98.3
Quaternary ridge crest	33	0.33	101.5
	33	0.32	104.6[2]*
	34	0.29	94.8
	35	0.26	88.2
	36	0.24	80.7
	37	0.22	76.2
	38	0.20	73.3

[1] High score parameters of ridge crest, on boundary of explored space.
[2] High score parameters of ridge crest, nonboundary maximum.
*Parameters selected for final evaluation.

The primary ridge ranged from L_{inf} = 43 mm, K = 0.50 to a boundary maximum at L_{inf} = 50 mm, K = 0.37. The highest nonboundary score was at L_{inf} = 48.0 mm, K = 0.40. A secondary ridge ranged from L_{inf} = 35 mm, K = 0.50 to L_{inf} = 50, K = 0.21, with a nonboundary maximum score at L_{inf} = 42.0, K = 0.30. A tertiary ridge ranged from L_{inf} = 32 mm, K = 0.50 to L_{inf} = 43 mm, K = 0.20, with a nonboundary maximum at L_{inf} = 32 mm, K = 0.49. A quaternary ridge ranged from L_{inf} = 33 mm, K = 0.33 to L_{inf} = 38 mm, K = 0.20, with a nonboundary maximum score at L_{inf} = 33 mm, K = 0.32 (Table 6, Fig. 13).

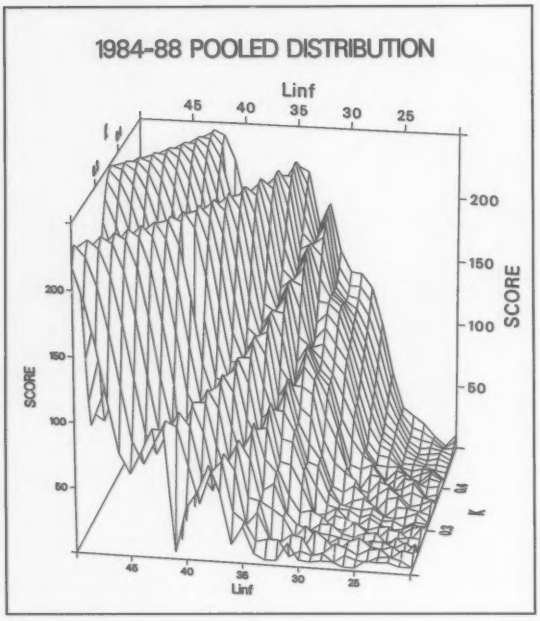

Figure 13
Response surface of the SRLCA score function for the northern shrimp survey 1984–88 length-frequency distribution.

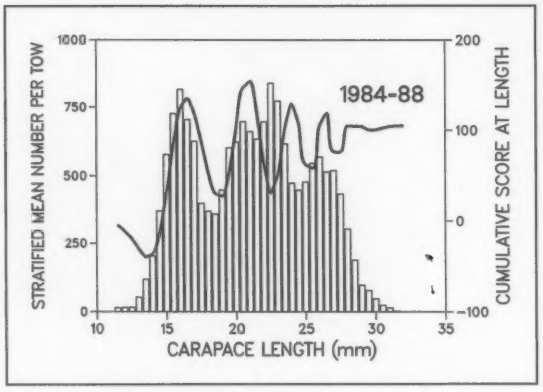

Figure 14
Northern shrimp survey 1984–88 pooled length-frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (L_{inf} = 33 mm, K = 0.32).

Values from the primary ridge tended to treat the assumed first and second observed age-groups, up to 21 mm, as a single mode, with animals greater than 21.5 mm classified as age 2. Values from the secondary ridge accurately interpreted the assumed age-group 1, but lumped the assumed second and third age-groups as a single mode, with shrimp >25 mm classified as age 3. Values from the tertiary ridge also correctly characterized the first age group and failed to resolve the second and third modes to distinct age classes, but split shrimp >24 mm into age-groups 3 and 4. It is interesting to note that the two sets of previously derived von Bertalanffy parameters for this stock noted earlier (see Methods: *A Priori* Assumptions) fell within this tertiary ridge of scores. This indicated that growth rates based on those parameters were too fast to provide an interpretation of length distributions consistent with visual inspection of the length modes.

Quaternary ridge values successfully classified the first–fourth assumed age-groups in line with prior assumptions. These parameters also provided an age-group 5 for CL >27.5 mm. The quaternary ridge non-boundary maximum score parameters (L_{inf} = 33 mm, K = 0.32) were selected for final SRLCA evaluation of the pooled length frequency, as these values provided the characterization of the pooled distribution closest to the assumed age structure (Fig. 14). The growth curve defined by these parameters indicates a slower rate compared with previously estimated growth curves (data from Haynes and Wigley 1969, McInnes 1986), a result of the influence, or "bias," of the abundant, apparently slower-growing, 1982 cohort on the score function (Fig. 15).

We derived annual age frequencies by slicing annual length frequencies to age-groups according to the maximum-scoring growth parameters provided by the four score ridges of the pooled analysis (Table 6). Since shrimp of age-group 2 and older are assumed fully recruited to the survey trawl gear, total instantaneous mortality estimates (Z) were derived from:

$$Z = \ln\left(\sum \text{age } 2+ \text{ for Year}_N \,/\, \sum \text{age } 3+ \text{ for Year}_{N+1}\right).$$

These values were then compared with previously calculated estimates of total mortality from the length-frequency data (NSTC 1985, 1986, 1987, 1988).

Table 7 shows the widely divergent age frequencies and subsequent Z estimates provided by the four different pairs of growth parameters, which again illustrate a necessity for some external source of information to interpret SRLCA results in a manner consistent with a priori assumptions. We note that for the 1987 distribution, the quaternary ridge parameters and NSTC visual inspection sliced the length-frequency distribution at the same length intervals, resulting in identical age frequencies for 1987. As expected, use of the quaternary SRLCA score ridge parameters to

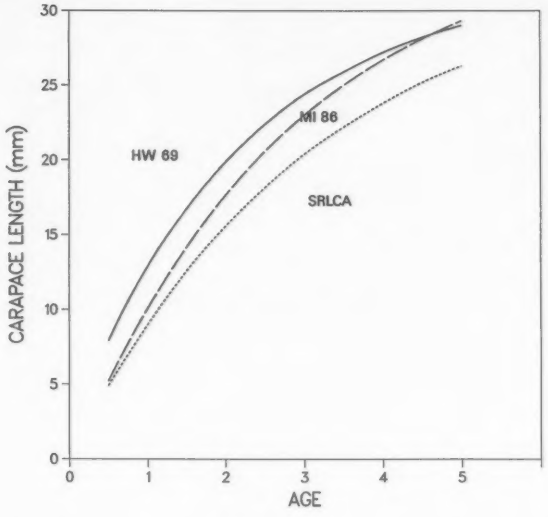

Figure 15

Von Bertalanffy growth curves for Gulf of Maine *Pandalus borealis*. Upper curve (solid line) is for parameters derived from age-length data in Haynes and Wigley (1969); center curve (large dashed line) is for growth parameters cited in McInnes (1986); lower curve (dot-dashed line) is for parameters derived by SRLCA for northern shrimp survey length-frequency data.

age the length frequencies provided mortality estimates consistent with those produced by visual inspection of length modes.

Discussion

We subjected SRLCA to a fairly stern test by attempting to interpret a data set exhibiting variable recruitment and growth patterns, and by using a broad initial parameter search space. As noted in the Monte Carlo tests of SRLCA by Basson et al. (1988), these variations in recruitment, and in mean length-at-age (presumed variable growth rate, especially for the abundant 1982 cohort) between cohorts, made interpretation of the northern shrimp length-frequency distributions difficult. The shape and proximity of the assumed age-2 and -3 modes frequently caused SRLCA to interpret these modes as a single age-group, resulting in highest scoring parameters that provided positively biased estimates of growth rate. This problem was most severe for the annual distributions and persisted in the pooled length frequency, although the increased amount of information in the pooled distribution did increase the effectiveness of the SRLCA approach, with a "correct" interpretation of the data available from the quaternary score ridge. Analysis of the pooled data in a truly sequential fashion, after the projection matrix approach of Rosenberg et al. (1986) and Basson et al. (1988), as a supplement to SRLCA might help in alleviating these problems.

This exercise demonstrated that the best objective fit obtained by SRLCA does not necessarily provide the best interpretation of the data, as with most of the existing length-frequency distribution analysis methods. Pragmatically, we could not rely on SRLCA to provide a single set (or even region) of growth parameters that yield both the highest parameter score and the "correct" interpretation of the data, unless supple-

Table 7

Age-frequency matrices and instantaneous total mortality rates (Z) for age 2+ northern shrimp estimated by growth parameters from SRLCA high-score parameter ridges for the 1984–88 pooled distribution, compared with estimates using method of visual inspection of length modes (NSTC 1984, 1985, 1986, 1987, 1988).

Age	1984	1985	1986	1987	1988
SRLCA					
Primary score ridge					
1	2150	887	1489	1091	3192
2	856	2644	1872	1357	1136
3	0	0	0	0	0
4+	0	0	0	0	0
	Z_{85} = ---	Z_{86} = ---	Z_{87} = ---	Z_{88} = ---	
Secondary score ridge					
1	633	660	753	575	2903
2	2001	2083	1504	1257	818
3	373	789	1104	620	604
4+	0	0	0	0	0
	Z_{85} = 1.10	Z_{86} = 0.96	Z_{87} = 1.44	Z_{88} = 1.13	
Tertiary score ridge					
1	672	660	755	577	2906
2	1853	1849	1283	1088	693
3	410	876	857	545	504
4+	71	146	465	239	224
	Z_{85} = 0.83	Z_{86} = 0.78	Z_{87} = 1.20	Z_{88} = 0.94	
Quaternary score ridge					
1	193	634	701	539	2564
2	1987	350	845	575	632
3	425	1710	615	663	433
4+	401	837	1200	671	699
	Z_{85} = 0.10	Z_{86} = 0.47	Z_{87} = 0.69	Z_{88} = 0.52	
NSTC					
Visual inspection					
1	49	646	710	539	2828
2	2051	337	959	575	614
3	442	1596	491	663	187
4+	463	952	1200	671	699
	Z_{85} = 0.15	Z_{86} = 0.53	Z_{87} = 0.69	Z_{88} = 0.77	

mented by an external source of information. For SRLCA to be effective, the subjectivity required in the selection of input parameters for use with the family of distribution mixture methods (e.g., MacDonald and Pitcher 1979) must instead be applied to interpretation of the output of the procedure.

These problems are similar to those encountered by others in evaluating the ELEFAN I method of Pauly and David (1981). Testing of ELEFAN I has indicated it produces biased results unless the range of growth parameters considered for testing is relatively narrow, and that it is sensitive to increased variation in length-at-age or increased variation in recruitment timing (Rosenberg and Beddington 1987). Recent work by Morgan (1987), supplementing ELEFAN with age-length data, improved the performance of that method by allowing selection of the appropriate parameters from among several locally optimal solutions.

We are encouraged, however, that such external information requirements were moderate for SRLCA. For instance, with an expectation of age of the oldest cohort, we would have immediately selected the quaternary ridge of the pooled analysis as best. Or, had we limited the initial search space for L_{inf} to within 10% of the CL of the largest animal, and/or 10% of an "average" L_{inf} given previously derived parameters (e.g., 33 ± 2 mm), we again could have proceeded directly to selection of the appropriate score ridge.

Even given conditions of variable growth and recruitment, we were able to inspect the response surface of the test function and, using a moderate degree of subjectivity and a stepwise procedure of evaluation, select growth parameters from alternative high-score ridges that resolved the pooled distribution in a manner consistent with previous interpretations, and, more important, in a more satisfactory manner than previously derived von Bertalanffy growth parameters. Overall we found SRLCA to be a simple and generally effective tool for the estimation of growth parameters, and subsequently age frequencies, from length-frequency distributions for Gulf of Maine northern shrimp.

Acknowledgments

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Annual Cycles of Gonad-Somatic Indices as Indicators of Spawning Activity for Selected Species of Finfish Collected from the New York Bight

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Abstract.—Gonad-somatic index (GSI), the relation of ovarian to somatic weight, was calculated for 14 species of finfish that are yearlong residents of the New York Bight. Specimens were collected monthly from June 1974 through June 1975 in the ocean and associated estuarine waters of the Bight. Analysis indicated that alewife and yellowtail flounder are spring spawners; silver and red hake, black sea bass, butterfish, striped and northern searobin, and fourspot flounder are summer spawners; and summer and winter flounder are fall-winter spawners. Offshore hake exhibited a protracted spawning season with ripe females collected from spring through fall, while spotted hake and windowpane exhibited bimodal spawning patterns with two GSI peaks per year. The co-occurrence of spawning with appropriate food supply and environmental conditions is discussed on an individual-species as well as species-complex basis.

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Fishery Bulletin, U.S. 88:775–786.

In temperate zones, reproduction of marine fish species is usually characterized by single annual peaks of spawning activity (Cushing 1969). Seasonal changes in the gonads of fishes, in preparation for reproduction, are known to be controlled by hormones, and triggered, sometimes well in advance of spawning, by photoperiod (Hoar 1969, Bye 1984). Minor variations in spawning time, during any given year, are believed to be related to temperature and to the overall condition of the fish (de Vlaming 1972, Bye 1984). Wootton (1984) defines reproductive "strategies" as the genetically determined pattern of spawning behavior, and reproductive "tactics" as the responses to exogenous cues during a single season.

The gonad-somatic index (GSI), the relation of ovarian weight to somatic weight, provides a measure of spawning readiness while removing variability attributable to fish size (Nikolskii 1963). The GSI has also been termed the gonosomatic index (de Vlaming et al. 1982) and maturity index (Morse 1981). Annual cycles in GSI can be thought of as an approximate measure of the energy expended for reproduction, which makes this information critical in formulating energy budgets relating to the balance between fish production and consumption.

Approximate spawning times for the most common species which occur in the New York Bight have been established based on the distribution of eggs and larvae (Colton et al. 1979) and published life-history information (Grosslein and Azarovitz 1982). However, detailed qualitative and quantitative information on annual cycles of spawning as determined by examination of maturity stages is lacking for many, if not most, of these same species. This study presents monthly variations in GSI as they relate to hydrographic observations for 14 species of fish which represent many of the dominant fishes found on the Middle Atlantic continental shelf and in associated estuarine waters (Wilk and Silverman 1976ab, Wilk et al. 1977; Colvocoresses and Musick 1984).

Materials and methods

Fish were collected from June 1974 to June 1975 during monthly bottom surveys in the central portion of the New York Bight at the confluence of the Long Island, New York and New Jersey coastlines and the contiguous Sandy Hook-Lower-Raritan Bay estuary (Fig. 1). This area is characterized by seasonally intensive recreational and commercial fisheries and is influenced by a wide variety of anthropogenic activities (Gross 1976, Mayer 1982).

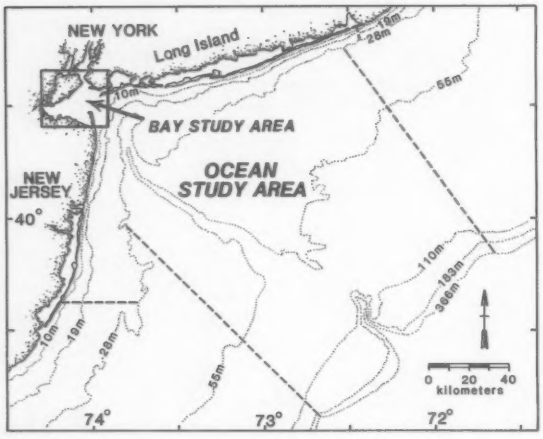

Figure 1

Middle Atlantic continental shelf with outlines of the ocean and estuarine (bay) study areas where finfish were sampled during a trawl survey of the New York Bight, June 1974–June 1975.

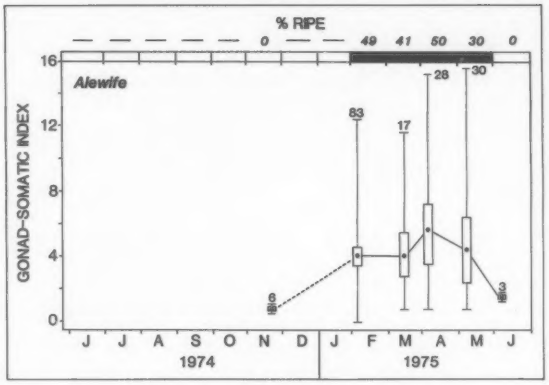

Figure 2

Annual cycle of gonad-somatic indices for alewife *Alosa pseudoharengus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

Two study areas, ocean and estuarine, were designated (Fig. 1). The ocean area was delineated by an imaginary set of lines extending seaward from points on Long Island, New York and New Jersey to the 28-m isobath and from the 28-m isobath to the edge of the continental shelf (366 m). This area corresponds to offshore strata 1–4 and inshore strata 6–17 of the Northeast Fisheries Center's resource trawl survey (Grosslein 1969). The estuarine study area included Sandy Hook, Lower, and Raritan bays.

Station locations in the ocean study area were selected by stratified random sampling design (Grosslein 1969). Strata boundaries were determined by depth as follows: 0–10, 11–19, 20–28, 29–55, 56–110, 111–183, and 184–366 m. A minimum of two stations per stratum was selected randomly to be sampled during each cruise. Inshore (0–28 m) and offshore (29–366 m) strata were sampled at rates of approximately one station per 515 and 1030 km^2, respectively. An average of 49 ocean stations was sampled per cruise. Ocean stations were not sampled during December 1974 and January 1975.

The estuarine study area was divided into 103 potential sampling blocks. Except where interrupted by land, each block measured 1′ of latitude by 1′ of longitude, i.e., 1.8 km × 1.4 km (2.5 km^2). A set of stations was selected randomly from these blocks and retained throughout the study. An average of 15 estuarine stations was sampled per cruise. Estuarine stations were not sampled during December 1974.

Fish collections were made with otter trawls towed at approximately 6.5 km/hour for 15 and 30 minutes at estuarine and ocean stations, respectively. Estuarine stations were sampled with a 9.1-m trawl and ocean stations with a Yankee #36 trawl. All specimens of each species, up to 35 individuals from each trawl station, were selected and frozen for later laboratory analysis. If the total catch of a species exceeded 35 individuals, a size-stratified sample of 25 to 35 specimens was frozen. At the laboratory each specimen was measured from the snout to the extent of the middle caudal fin ray (±1.0 mm), weighed (±0.1 g), sexed, and state of maturity determined by macroscopic evaluation when possible. Stage of ovarian development was determined visually, and designated immature, developing, ripe, or resting. Ovaries were weighed (±0.01 g) and GSI calculated (ovarian weight/fish weight × 100). It should be noted that only mature females were included in the calculation of GSI.

Temperature and depth observations were made at all stations. Vertical temperature profiles were obtained with expendable bathythermographs during ocean cruises and with portable temperature probes during estuarine cruises. Fathometers continually recorded depth during each trawl tow. Detailed information relative to survey design, methodology, species distribution and abundance, and associated hydrographic observations is given in Wilk et al. (1977).

Results

The majority (93%) of all ripe females collected during the survey were caught in the ocean study area. Of the

Table 1

Observations relative to peak spawning activity for 14 finfish species, including mean and range of bottom temperature and depth for the month, or months, of highest gonad-somatic indices (GSI) at stations where ripe females occurred during a trawl survey of the New York Bight, June 1974–June 1975. Alewife and winter flounder data include only estuarine observations; bimodal spawners are indicated with an asterisk (*) with observations given for both peaks; in some cases months were combined when sample sizes were small.

Species	Month	No. of fish	Occurrence/total no. of stations	Bottom temperature (°C)		Depth (m)	
				Mean	Range	Mean	Range
Alewife	Apr 75	18	7/14	5.4	4.5–6.0	6	5–11
Offshore hake	May/Jun 75	17	4/156	10.2	9.0–11.4	270	222–348
Silver hake	Aug 74	5	4/58	9.8	8.4–13.4	80	54–127
Red hake	Jun 75	68	23/72	8.0	5.7–12.5	60	12–264
Spotted hake*	Sep 74	42	7/56	14.8	11.0–17.3	30	12–86
Spotted hake*	Mar/Apr 75	10	4/109	10.5	7.4–12.3	113	75–139
Black sea bass	Jul 74	16	3/59	14.9	13.8–15.9	19	16–22
Butterfish	Jun 74 & 75	189	45/130	11.8	5.4–20.4	40	3–145
Northern searobin	Jul 74	21	8/59	15.1	13.8–16.5	20	15–27
Striped searobin	Jun 74 & 75	12	8/130	10.9	8.4–14.1	16	9–21
Summer flounder	Oct 74	51	22/60	13.7	10.5–14.7	35	11–97
Fourspot flounder	Jun 75	32	15/72	7.3	5.6–11.2	57	17–127
Windowpane*	Sep 74	150	23/56	15.7	10.3–19.4	26	10–65
Windowpane*	May 75	159	44/84	7.9	5.6–13.2	23	4–51
Yellowtail flounder	Mar 75	45	15/46	5.7	4.4–7.5	36	9–68
Winter flounder	Jan 75	5	3/9	5.7	4.8–6.5	5	3–7

total catch of ripe female alewife and winter flounder, 5 and 21%, respectively, were collected in the estuarine study area. This was expected since these species are known to inhabit the lower reaches of estuaries before moving upriver to spawn. Ripe female butterfish and windowpane were also collected in the estuarine study area, but made up <5% of the catch of all ripe females of those species. Eggs and larvae of these four species are known to occur in both Raritan Bay (Croker 1965) and the New York Bight (Clark et al. 1969; Smith et al. 1975, 1980). Silver hake, red hake, and summer flounder were also caught in the estuarine study area during some months; however, no ovarian development beyond the resting stage was observed. All data were pooled since there were no clear differences in time of spawning between bay and ocean samples of any species captured during the study. Detailed results and discussion for each species are given in the following sections.

Alewife *Alosa pseudoharengus*

Mean GSI was highest in April, with ripe females, 145–345 mm, collected throughout the survey area from February through May (Fig. 2). These observations are similar to published spawning times for alewife in Connecticut inshore waters (Kissil 1969) and the Delaware River (Smith 1971). Farther north in Canadian waters the species spawns primarily in May (Leim and Scott 1966).

Alewives are common in coastal waters from Newfoundland, Canada to North Carolina as they migrate to and from their riverine spawning grounds (Hildebrand and Schroeder 1928, Bigelow and Schroeder 1953, Leim and Scott 1966). The average temperature in the estuarine survey area during the April spawning peak was 5.4°C (Table 1).

Offshore hake *Merluccius albidus*

Mean GSI was highest during July 1974 and again in June 1975, with ripe females, 230–575 mm, collected in ocean waters during most months sampled (Fig. 3). The highest percentages of ripe ovaries were observed in spring and summer. In a review of historic ichthyoplankton surveys, Colton et al. (1979) stated that offshore hake larvae were present in the Middle Atlantic from June through September. Smith et al. (1980) collected eggs and larvae south of New England from April through June during 1977–79 ichthyoplankton surveys. They also collected eggs in late February–early March 1979 from stations south of Long Island, New York. Marak (1967) found eggs and larvae off Martha's Vineyard, Massachusetts, in April through July. Offshore hake, based on this as well as the aforementioned studies, has either a long or irregular spawn-

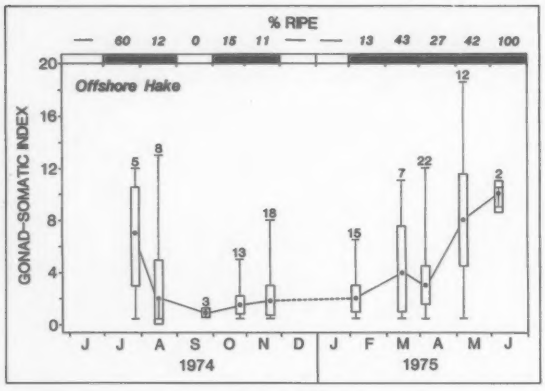

Figure 3

Annual cycle of gonad-somatic indices for offshore hake *Merluccius albidus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

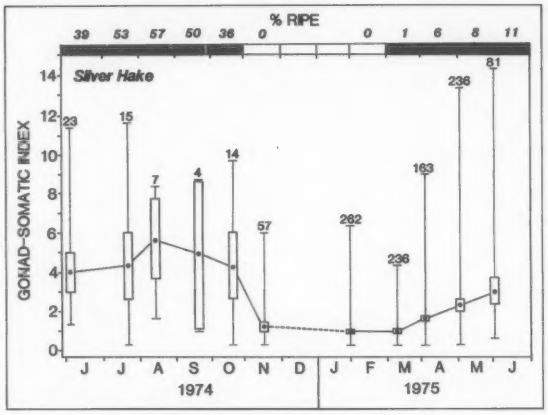

Figure 4

Annual cycle of gonad-somatic indices for silver hake *Merluccius bilinearis* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

ing season or perhaps even spawns continually throughout the year.

Offshore hake range from Georges Bank to the coast of South America along the continental shelf break in depths >100 m (Bigelow and Schroeder 1955, Leim and Scott 1966). They are the deepest ranging species described in this study, being found between 162 and 366 m, the survey extreme. They were collected within a relatively restricted temperature range throughout the year, with little or no seasonal changes.

Silver hake *Merluccius bilinearis*

Ripe females, 202–590 mm, were collected in ocean waters during a long spawning season, March through October, with mean GSI highest from July to October (Fig. 4). A protracted spawning season for this species in the Middle Atlantic is supported by two ichthyoplankton surveys: (1) Fahay (1974) collected eggs during 1966 from May through November with a peak in June–July; and (2) Sherman et al. (1984) reported larvae were collected during 1977–79 from April through November, with a peak in August.

Silver hake are found over all bottom types from the intertidal zone to the 200-m isobath from Nova Scotia, Canada to Cape Hatteras, North Carolina (Bigelow and Schroeder 1953, Leim and Scott 1966). During August, the month of highest mean GSI, silver hake were found well offshore where temperatures were moderate (Table 1). During the remainder of the year females were captured throughout the entire survey area at a wide variety of depths (4–335 m) and temperatures (4.3–19.2°C).

Red hake *Urophycis chuss*

Mean GSI was highest during the summer; however, ripe females, 225–621 mm, were present from May through September (Fig. 5). Colton et al. (1979) reported the occurrence of larvae in the Middle Atlantic from May through October with a peak in June or July. Off the southern New England coast, adults migrate offshore to the continental slope and spawn during May through September at temperatures of 5–11°C (Musick 1969, 1974).

Red hake were among the deepest spawners observed during the study with a mean capture depth of 60 m in June 1975 during the height of the spawning cycle (Table 1). The mean temperature of 8.0°C at time of spawning agrees with previously reported observations. It is noteworthy that five specimens in spawning condition were caught at two nearshore ocean stations at which the depth and temperature were 25 and 27 m and 15.3 and 17.1°C, respectively. These observations, to some degree, broaden the spawning depth and temperature ranges reported by Musick (1969, 1974).

Spotted hake *Urophycis regia*

Spotted hake exhibited a bimodal or split spawning pattern which was characterized by two mean GSI peaks,

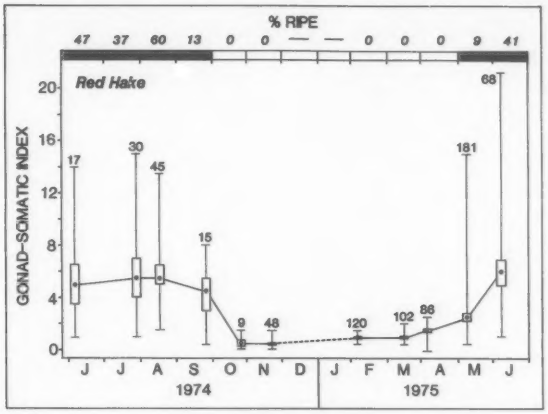

Figure 5

Annual cycle of gonad-somatic indices for red hake *Urophycis chuss* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

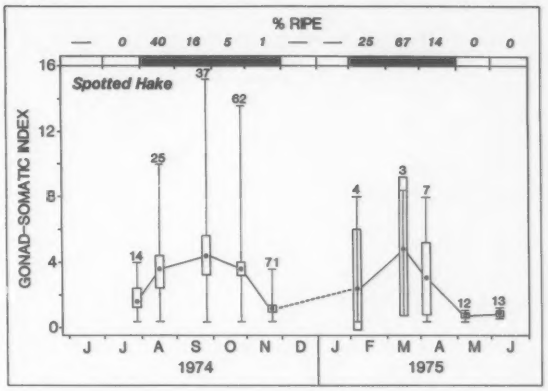

Figure 6

Annual cycle of gonad-somatic indices for spotted hake *Urophycis regia* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

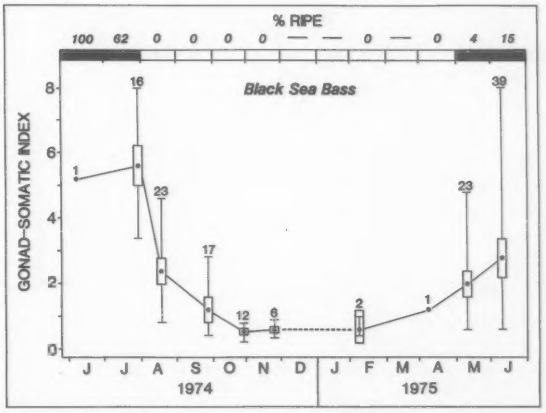

Figure 7

Annual cycle of gonad-somatic indices for black sea bass *Centropristis striata* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

one during March followed by another in September (Fig. 6). Ripe females, 283–396 mm, were collected from February through April. In addition, ripe females, 191–360 mm, were present again from August through November. Colton et al. (1979) suggested a spawning time of August through April with an October peak, but did not allude to a bimodal spawning pattern. Barans (1969) observed ripe females, with a minimum length of 225 mm, in the Chesapeake Bight from August through November. In collections made off the Carolinas, ripe spotted hake were found during December (Bigelow and Schroeder 1953).

In the September sample, ripe females were caught at depths between 12 and 86 m and temperatures of between 11.0 and 17.3°C. In contrast, during March and April ripe females were caught at much deeper and cooler locations (Table 1). Spotted hake range from southern New England to Florida (Hildebrand and Schroeder 1928, Bigelow and Schroeder 1953); however, they are most abundant south of Chesapeake Bay (Barans 1969). In the Chesapeake Bight, Barans (1969) reported their temperature range as 6–20°C, with a preferred range of 10–12°C. In addition, he gave 190 mm as the minimum length for 1-year-old females, and >280 mm for 2-year-olds. If the spotted hake captured during this study follow the size at ages given by Barans (1969), the population present in spring is composed primarily of older fish, with young-of-the-year and yearlings migrating into the area during summer and fall. The apparent split spawning season observed during this study may be attributable to dissimilar distributional patterns of specific age groups at the northernmost extreme of the species range.

Black sea bass *Centropristis striata*

Mean GSI was highest during July, with ripe females, 184–452 mm, collected from May through July (Fig. 7). Black sea bass are protogynous hermaphrodites with the size at which females become males extremely

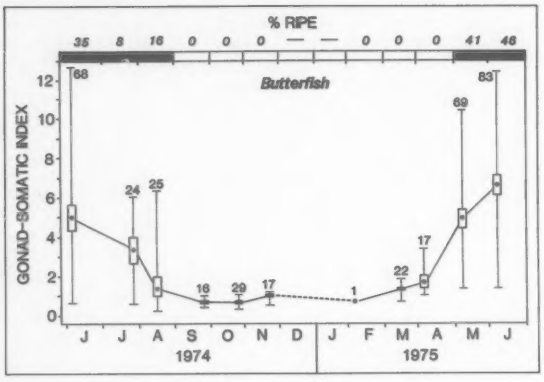

Figure 8

Annual cycle of gonad-somatic indices for butterfish *Peprilus triacanthus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

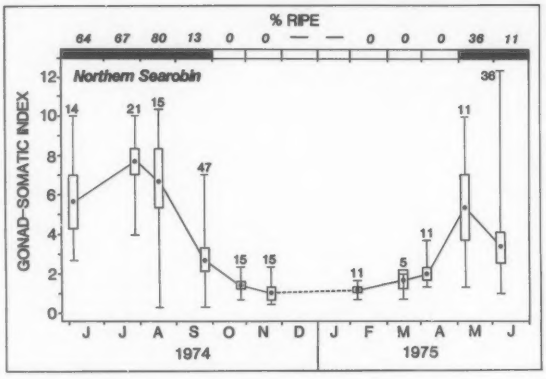

Figure 9

Annual cycle of gonad-somatic indices for northern searobin *Prionotus carolinus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

variable (Kendall and Mercer 1982). In this study female and male black sea bass were in the range 173–452 and 178–556 mm, respectively. Bigelow and Schroeder (1953) reported spawning from mid-May through June off southern New England and New Jersey. To date, black sea bass eggs have not been reported from plankton collections. However, larvae have been collected from Long Island, New York waters from mid-May to June (Perlmutter 1939) and from offshore New York Bight waters from June through November (Kendall 1977).

Black sea bass are common from Cape Cod, Massachusetts to Florida (Hildebrand and Schroeder 1928, Bigelow and Schroeder 1953). In the Middle Atlantic, they migrate northward and inshore in spring and offshore and southward in fall (Kendall and Mercer 1982). Mean temperature and depth of occurrence in July, the month of highest mean GSI, were among the warmest and shallowest of the survey (Table 1).

Butterfish *Peprilus triacanthus*

Highest mean GSI occurred in June 1974 and again in May and June 1975, with ripe females, 124–242 mm, being present throughout the survey area from May through August (Fig. 8). The butterfish is a migratory semi-pelagic species which ranges from Newfoundland, Canada to Florida (Bigelow and Schroeder 1953, Leim and Scott 1966). Colton et al. (1979) reported butterfish spawning in the Middle Atlantic from May through October with a peak in July or August. Smith et al. (1980) collected eggs off North Carolina during spring and larvae off New Jersey during early summer. Kawahara (1978) reported the spawning time of butterfish in the Middle Atlantic as April or May through August. Butterfish were collected at a wide range of temperatures and depths during the months of peak GSI (Table 1).

Northern searobin *Prionotus carolinus*

Highest mean GSI was in July; however, ripe females, 143–341 mm, occurred from May through September (Fig. 9). According to Richards et al. (1979), based on data from the north shore of Long Island, New York, GSI rose early in May, peaked in late May, and declined gradually through June and July. Colton et al. (1979) reported spawning from Block Island, Rhode Island to Cape Hatteras, North Carolina from May through November.

Eggs and larvae of *Prionotus* spp. are among the dominant ichthyoplankton occurring in the Middle Atlantic from New Jersey to Cape Hatteras, North Carolina during June through October (Smith et al. 1980, Sherman et al. 1984). This survey demonstrated that northern searobin favored warm shallow inshore waters during peak spawning (Table 1); however, from November through April they favored depths >50 m.

Striped searobin *Prionotus evolans*

Highest mean GSI occurred during June and July 1974 and again in June 1975, with ripe females, 204–414 mm, present from May through August (Fig. 10). Richards et al. (1979) determined spawning time for striped searobin to be almost the same as northern

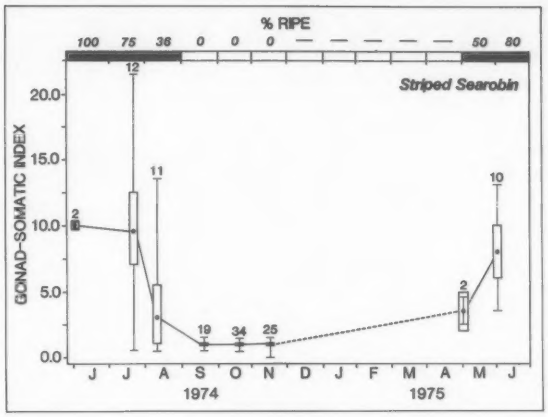

Figure 10

Annual cycle of gonad-somatic indices for striped searobin *Prionotus evolans* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

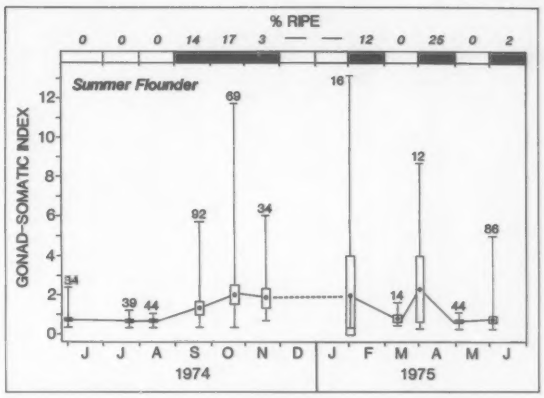

Figure 11

Annual cycle of gonad-somatic indices for summer flounder *Paralichthys dentatus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

searobin. Perlmutter (1939) collected larvae off Long Island, New York between May and June; and Herman (1963) reported spawning from June through August off Narragansett Bay, Rhode Island.

This study indicated temperature preferences during spawning were somewhat cooler than those of the northern searobin, while depths were similar (Table 1). However, throughout the remainder of the year, striped searobin were collected in comparatively warmer and shallower waters than northern searobin.

Summer flounder *Paralichthys dentatus*

Ripe females, 309–716 mm, were collected from September through November, and sporadically from February to June (Fig. 11). Although there were several slight peaks in GSI during the spawning season, these probably resulted more from individual sample variability than actual peaks in spawning activity (Fig. 11). Morse (1981), using additional maturity data from the New York Bight, reported spawning from September through March with a peak in October. Smith (1973) reported that eggs and larvae began to appear in September off Long Island, New York and southern New England, and occurred farther southward as fall progressed. After December, recently hatched larvae were common only south of Chesapeake Bay (Smith 1973).

Summer flounder range between Nova Scotia, Canada and Florida with their center of abundance lying in the Middle Atlantic region (Leim and Scott 1966, Gutherz 1967, Wilk et al. 1980). They migrate to shallow coastal waters and bays in summer, then offshore in fall (Bigelow and Schroeder 1953). At the GSI peak in October, developing females were collected in relatively warm shelf waters (Table 1). Depths of collection for summer flounder varied during the year, from a mean of 11 m in July to 92 m in April, reflecting their seasonal migration pattern.

Fourspot flounder *Paralichthys oblongus*

Mean GSI were highest in June and July 1974 and again in June 1975, with ripe females, 153–419 mm, present from April through September (Fig. 12). Smith et al. (1975) found small larvae off North Carolina and Chesapeake Bay in May and June, and off New Jersey and New York in July and August.

Fourspot flounder are widely distributed on the continental shelf between Georges Bank and Cape Hatteras, North Carolina (Bigelow and Schroeder 1953, Gutherz 1967). In the New York Bight, they inhabit the entire shelf, with deepest occurrences during winter (Ralph 1982). Collections from this survey indicate they were deepest during February and March, averaging 90 and 92 m, respectively, moving somewhat inshore during the rest of the year, but always at depths averaging >40 m. They were collected over a wide range of depths and temperatures during the June spawning peak (Table 1). Smith et al. (1975) collected larvae between 6 and 9°C at depths of 35–80 m.

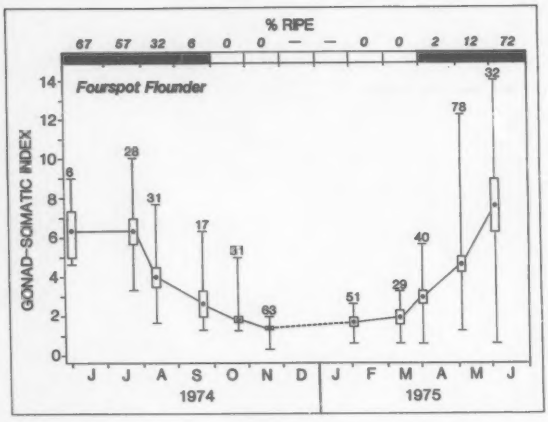

Figure 12

Annual cycle of gonad-somatic indices for fourspot flounder *Paralichthys oblongus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

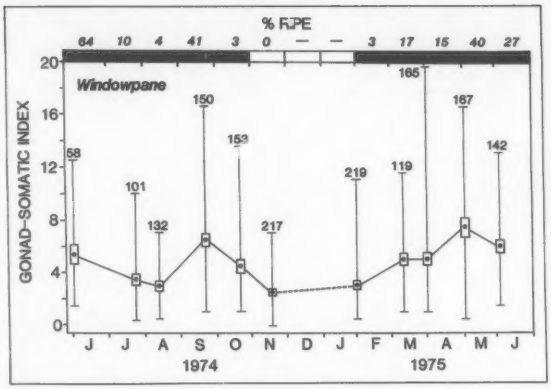

Figure 13

Annual cycle of gonad-somatic indices for windowpane *Scophthalmus aquosus*, collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

Windowpane *Scophthalmus aquosus*

The GSI plot for windowpane was bimodal, with peaks in May and again in September (Fig. 13). Ripe females, 201–387 mm, were collected from February through October, indicating that windowpane may spawn to some degree in the New York Bight during most of the year. Unfortunately, data for winter are lacking. There was no conclusive evidence that the two peaks represented spawning of either different populations or age classes. In September the mean lengths were 261 and 230 mm for females and males, respectively; in May, windowpane were somewhat more abundant and larger with mean lengths of 285 and 247 mm for females and males, respectively.

Split spawning of windowpane has been reported previously in the Middle Atlantic region. In 1952 and 1953, Wheatland (1956) found eggs from May through early July and again from late September through November in Long Island Sound, New York. Temperatures in the Sound were >20°C from late July through September when eggs were not present. Smith et al. (1975) proposed two patterns of spawning for windowpane depending on latitude. First, off New Jersey and New York one prolonged spawning season was hypothesized based on the occurrence of 2–6 mm larvae on the inner shelf from June through December 1966. Bottom temperatures on the inner shelf that year ranged between 6 and 17°C during August (Clark et al. 1969). Second, off Virginia and North Carolina spawning was interrupted as indicated by the occurrence of larvae in April through June and again in November and December 1966. During summer 1966 bottom temperatures ranged between 15 and 25°C (Clark et al. 1969). Smith et al. (1975) therefore concluded that in waters >20°C windowpane stop spawning.

Windowpane were collected during the May GSI peak at 5.6–13.2°C and 4–51 m; while during the September peak they were collected at higher temperatures but at similar depths (Table 1). In July and August, when GSI decreased noticeably, maximum bottom temperatures were 20–22°C at nearshore stations. Based on the results of this survey, coupled with the previously cited historical observations, a split spawning season is probably typical for windowpane in the New York Bight with continuous spawning occurring only during unusually cold summers.

Yellowtail flounder *Limanda ferruginea*

Highest mean GSI occurred from February to April, with ripe females, 212–422 mm, collected in October and November and February through May (Fig. 14). Howell (1983) observed female yellowtail off Rhode Island beginning to mature in September, with the peak GSI in April. Colton et al. (1979) reported spawning in the Middle Atlantic from April through August with peaks in May and June. Smith et al. (1975) found the largest concentrations of larvae off New Jersey in April and May. They also reported larvae in abundance off southern New England in May and June.

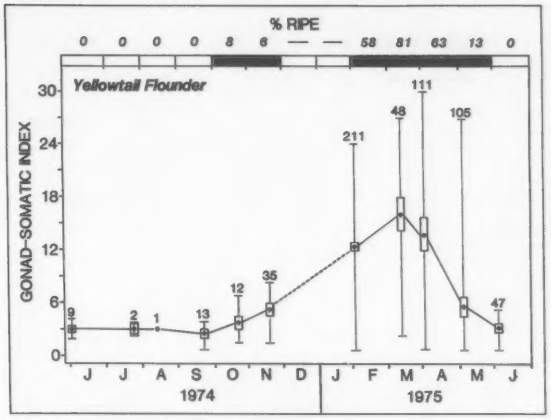

Figure 14

Annual cycle of gonad-somatic indices for yellowtail flounder *Limanda ferruginea* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

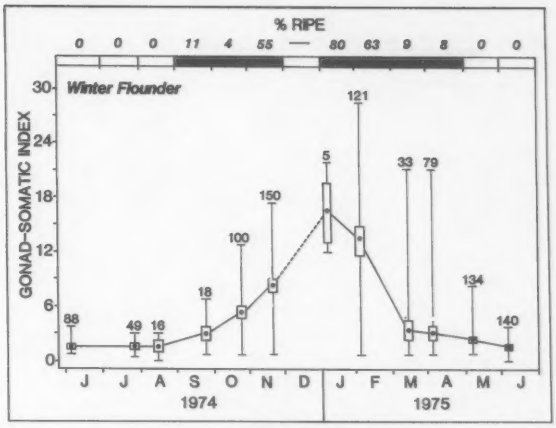

Figure 15

Annual cycle of gonad-somatic indices for winter flounder *Pseudopleuronectes americanus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

Yellowtail flounder commonly occur from Nova Scotia, Canada to Delaware Bay (Bigelow and Schroeder 1953, Leim and Scott 1966). Smith et al. (1975) considered the population center to be on Georges Bank, with migration along the southern New England shelf eastward in spring and westward in fall (Lux 1963). In the New York Bight, few were caught in summer. In March of this survey, the period of greatest gonad development, they were collected on the inner shelf at 9–68 m and 4.4–7.5°C (Table 1).

Winter flounder
Pseudopleuronectes americanus

Highest mean GSI occurred during January in the estuarine survey area and during February in the ocean survey area (Fig. 15). Ripe females, 169–432 mm, were collected from September through April with 21% occurring in Raritan Bay. GSI declined rapidly after February; however, spawners were likely upriver beyond the range of this survey. Smith et al. (1975) captured larvae at inshore stations between the offing of Delaware Bay and Block Island Sound, Rhode Island from April through June, with spawning beginning in the south and progressing northward. Perlmutter (1947) reported spawning from December through May and concluded that the peak time varied with temperature. Pearcy (1962) found evidence of spawning from mid-February through April in the Mystic River estuary, Connecticut. Croker (1965) found winter flounder larvae in plankton collections in Sandy Hook Bay, New Jersey from April to June.

Although the water temperature at actual spawning sites is unknown, the average bottom temperature in Raritan Bay during January, the month of highest mean GSI, was 5.7°C. Of all the species encountered during this survey, winter flounder were collected in the coldest water.

Discussion

According to Braum (1978), most temperate zone fishes spawn in one of three generic seasonal patterns: spring, summer, or fall-winter. Based on the current study, alewife and yellowtail flounder are spring spawners; silver and red hake, black sea bass, butterfish, northern and striped searobin, and fourspot flounder are summer to fall spawners, while spotted hake and summer and winter flounder are fall-winter through early spring spawners. Offshore hake and windowpane belong to none of these groups, but appear to have protracted spawning seasons, i.e., these species' GSI were elevated, ovaries were ripe, and eggs and larvae were collected from spring through fall. Offshore hake inhabit the deeper waters of the Bight which are less influenced by changes in light and temperature. In contrast, windowpane inhabit the shallow, more seasonally influenced, inshore environs.

In temperate seas, there are distinct annual cycles of light intensity, temperature, nutrients, and winds

which drive cycles of productivity. An abundant source of food must be available for adult fish to produce stored fat for subsequent gamete production (de Vlaming 1972). Plankton of the right size, density, and quality must be available to pelagic larvae at the critical time of first feeding. As an example, the spawning of yellowtail flounder corresponds to the spring increase in zooplankton off southern New England (Sherman et al. 1984). The maximum concentration of zooplankton in the Middle Atlantic occurs from mid- to late-summer which coincides with the peak concentrations of larval searobins and butterfish as well as numerous other species (Sherman et al. 1984). The fishes that reproduce in the New York Bight during winter have already accumulated fat reserves during the summer and fall. Releasing eggs during winter may give a survival advantage to the larvae since many other fishes, potential competitors and predators, have migrated from the area and there is, therefore, little competition at a crucial time of development.

A short spawning season, represented by a steep GSI curve with a single peak, is a common strategy in temperate marine zones. Black sea bass, butterfish, and the searobins had the shortest spawning seasons, with ripe fish present for only 3–5 months. These four species are abundant during summer in the Middle Atlantic (Wilk and Silverman 1976ab, Wilk et al. 1977, Colvocoresses and Musick 1984), but not on the more boreal Georges Bank (Overholtz and Tyler 1985). They were collected at the highest average temperatures during their reproductive peaks (Table 1). Most of the other species described are abundant in both regions and were collected in colder waters.

Sherman et al. (1984) describe a ubiquitous or protracted spawning strategy for certain species including silver hake and *Urophycis* spp., in which eggs are produced for several months and, although mortality is high, some larvae survive when environmental conditions and food supply are properly matched. In this study, ripe female offshore silver and spotted hake, as well as windowpane, summer, and winter flounder, were collected for 5 or more months. Eggs and small larvae of these species were observed for many more months in other surveys (Clark et al. 1969; Smith et al. 1975, 1980; Colton et al. 1979).

Eggs are typically released from the ovaries of fishes in batches (Bagenal 1978). In species with short reproductive periods, these batches are released in the span of a few days with all individual fish spawning at about the same time. In multiple or serial spawners, batches of eggs mature and are shed several times during a long spawning season (Bagenal 1978, Burt et al. 1988). Examples of protracted spawners are silver hake which produce as many as three batches of eggs per spawning season (Fahay 1974) and summer flounder which produce up to six batches (Morse 1981). Summer flounder had the lowest mean GSI of any species collected during this survey, apparently because their eggs develop in batches and are released over an extended period. In contrast, the highest mean GSI noted were for yellowtail and winter flounder which produce only one batch of eggs per season (Howell 1983, Burton and Idler 1984). In both species, GSI increased gradually in fall through winter as eggs matured, with highest GSI levels being reached just prior to spring spawning. Similarly, Burton and Idler (1984) reported that GSI of winter flounder in Canadian waters gradually rose during the 8 months before spawning takes place in June.

A high GSI does not always parallel a high level of fecundity (Bagenal 1978). As an example, larger summer, yellowtail, and winter flounder have exhibited fecundities of over 1 million (Bigelow and Schroeder 1953, Morse 1981, Lux and Livingstone 1982); egg production in each of these species is accomplished, however, on different timetables.

Spotted hake and windowpane, both protracted spawners, had bimodal GSI curves. Various sizes of developing and ripe female spotted hake were collected in fall, while a few large ripe females were collected in spring. These findings may reflect behavioral differences among size or age classes, or perhaps the migratory habits of discrete unit stocks. Windowpane exhibited two GSI peaks in the New York Bight during 1974–75; however, continuous larval production throughout the summer was noted in an earlier survey of the area (Smith et al. 1975). Windowpane are permanent residents in the Bight; that is, no evidence of seasonal migration was found during this survey based on observed changes in abundance, size structure, or distribution of collections. Rather than a result of emigration, the bimodal GSI curve exhibited by windowpane may very well be a result of a reproductive tactic in which spawning is curtailed during the year if temperature rises above a preferred level.

Some of the most important and prolific commercial fisheries taking place in temperate seas around the world are based on families of fishes, such as gadids (codfishes and hakes) and pleuronectids (flounders), that are typically very fecund and produce relatively small pelagic eggs (Garrod and Horwood 1984). Of the species described in this study, the pleuronectids, yellowtail and winter flounder, and the bothid, summer flounder, have been reported to have extremely high fecundities. Such species are well-suited for commercial exploitation since they can recover rapidly from natural or man-induced depletion. The gadids described in this study are all small-bodied, mature early at a relatively small size, and produce many tiny pelagic eggs over a protracted spawning period; however, they

are not as fecund as larger and more robust gadid species such as Atlantic cod *Gadus morhua* (Hislop 1984).

A variety of reproductive strategies and tactics are used by the species to adapt to seasonal shifts in environmental parameters in the Middle Atlantic in general and the New York Bight specifically. In this way the entire region is continually used for reproduction by a wide range of economically and ecologically important species of resident and migratory finfish. These spawning adaptations contribute to the high diversity and abundance of finfish found in the Middle Atlantic region.

Acknowledgments

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Three New Species of Hagfishes, Genus *Eptatretus* (Cyclostomata, Myxinidae), from the Pacific Coast of North America, with New Data on *E. deani* and *E. stoutii*

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Abstract.—Three new species of the genus *Eptatretus*–*E. mcconnaughey*', from off Southern California and Northern Baja California, and an isolated population in the southern portion of the Gulf of California; *E. fritzi*, known only from the immediate vicinity of Guadalupe Island, Mexico; and *E. sinus*, confined to the midriff area of the Gulf of California—are described. New data are presented for *E. deani* and *E. stoutii*. A neotype is designated for *E. stoutii*.

Despite the extensive ranges of *E. deani* (southeastern Alaska to Guadalupe Island, Mexico) and *E. stoutii* (Vancouver Island, Canada, to Pt. San Pablo, about 80 miles southerly from Cedros Island, Mexico), no appreciable differences were found in counts and body proportions within each species. However, the disjunct populations of *E. mcconnaugheyi* display significant differences ($P>0.001$) in numbers of trunk and total slime pores; in all other characters the two populations are very similar.

Sex ratios for four of the species are notably uneven, ranging between 60% and 74% female, 26% and 40% male. The sex ratio for *E. stoutii* is essentially even, 49% female and 51% male.

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Fishery Bulletin, U.S. 88:787–804.

This study continues our efforts on the genus *Eptatretus*, a part of the unfinished work of Carl L. Hubbs (deceased 30 June 1979). Two previous studies (McMillan and Wisner 1984, Wisner and McMillan 1988) and this have resulted in descriptions of seven new species of *Eptatretus*, two from off Central Chile, one each from the Hawaiian and Philippine areas, and three herein. Also, we have described a new species, *Nemamyxine kreffti*, from off Rio de Plata, Argentina (McMillan and Wisner 1984). In addition, a study on the genus *Myxine* is progressing, involving at least six new species from off the Atlantic and Pacific coasts of North and South America.

The present effort includes the largest amount of study material, about 2300 specimens. Many specimens of *E. stoutii* and *E. deani* are not included in the lists of material examined due either to poor preservation, to questionable capture data, or to a surfeit of material from an area, particularly off southern California. All specimens from near the extremes of ranges are included, as are all specimens of the three new species.

Due to the availability for the first time of large numbers of specimens of *E. stoutii* and *E. deani*, each having extensive distributions, we attempted to delineate an annual and spatial period of deposition (extrusion) of eggs for each. Capture data for females containing eggs of at least 20 mm length showed that eggs of this size were present in both species throughout the year throughout all areas of their ranges. The maximum lengths of eggs were 28.6 mm for *E. stoutii* and 52.3 for *E. deani*. Although these lengths may not indicate the ultimate lengths of eggs at time of deposition, it is very probable that deposition by both species occurs throughout the year and in all areas of their distributions.

Except for two collected in November, all specimens of *E. fritzi* were taken in April; eggs to 33 mm were present. Similarly, specimens of *E. sinus* were taken within two short periods, 20–22 January and 28 February–2 March eggs to 32 mm were present.

The occurrence and arrangement of head grooves (lateral lines of authors) in all species treated here agree well with those described and figured by Ayers and Worthington (1907:332–333, figs. 5, 6) and by McMillan and Wisner (1984:255, fig. 4).

Methods and materials

Methods of counting and measuring are those recommended by McMillan and Wisner (1984) and Wisner and McMillan (1988). Features used in

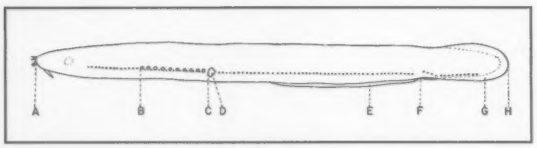

Figure 1

Outline of hagfish (*Eptatretus*) showing regions and features used in measuring and counting: A–H, total length (TL); A–B, prebranchial length; B–C, branchial length, including gill apertures (GA); D, external opening of pharyngocutaneous duct (PCD); E, ventral finfold; C–F, trunk length; F, origin of cloaca; F–H, tail length; G, caudal finfold. The linear series of dots represents the prebranchial, branchial, trunk, and cloacal-caudal (tail) slime pores.

counting and measuring are shown in Figure 1. Abbreviations used are given below and identified in Figure 4.

Abbreviations

ABA Afferent branchial artery; one of the small blood vessels that lead to each gill pouch from VA or its branches (Fig. 4).

DM Dental muscle; the firm elongate, cylindrical complex of muscles and cartilages that moves the dental plates and sets of cusps during feeding. Posterior portions of DM are shown in Figures 2–4, lying between rows of gill pouches.

GA Gill (branchial) aperture; external opening of the efferent duct leading from a gill pouch (Fig. 1).

GP Gill pouch; rounded, serially arranged structures along and posterior to the dental muscle (Fig. 4).

PCD External opening of the pharyngocutaneous duct; always confluent with the posteriormost left gill aperture in most species of *Eptatretus*, and much larger than all other apertures (Fig. 1).

VA Ventral aorta; the portion between the heart (ventricle) and to where it branches to each side of DM (Fig. 4).

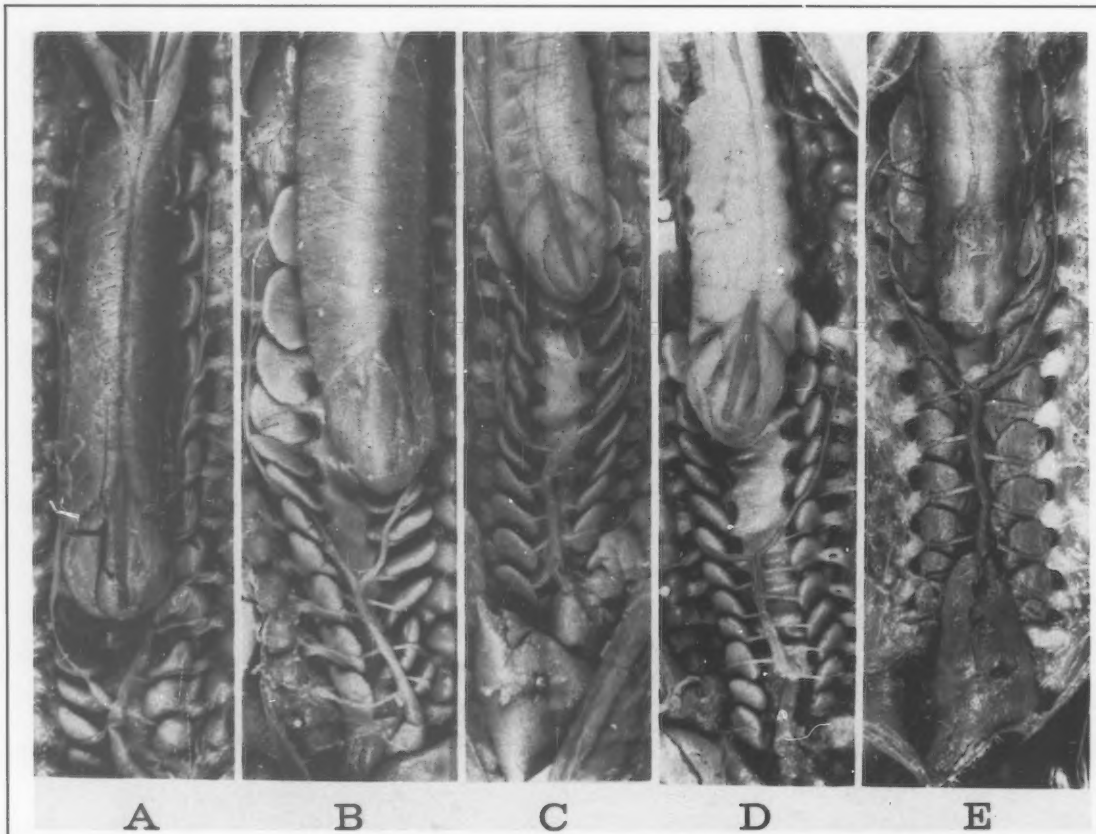

Figure 2

Branchial areas of holotypes of (A) *Eptatretus mcconnaugheyi*, (B) *E. fritzi*, and (C) *E. sinus*; (D) neotype of *E. stoutii*; (E) *E. deani*. The dental muscle (DM) is the cylindrical mass lying between the rows of gill pouches (GP).

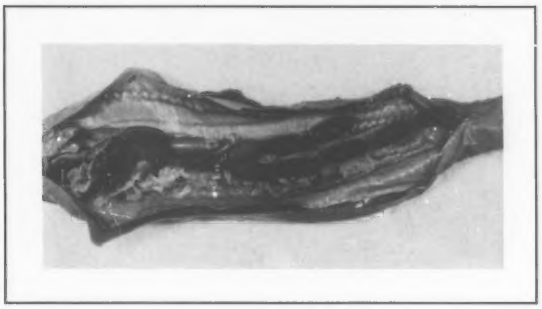

Figure 3
Mature eggs of holotype of *E. mcconnaugheyi* showing *in situ* arrangement and connections by anchor filaments (terminal hooks).

Other features used are:

Preocular length From center of left eyespot to center of rostrum.

Barbel length From crease at mesial base to tip of barbel.

Collection data and deposition of specimens are listed for each species. All specimens were taken on bottom, with a trap or trawl, except for two of *E. stoutii* taken by scuba divers near San Diego. Institutions which have provided study material, or in which type specimens are deposited, are SIO, CAS, LACM, MCZ, USNM, OSUO, BCPM, and UW. These symbolic institutional codes follow the usages in Leviton et al. 1985.

We introduce length of barbel as a systematic character. Barbels have not been used in the taxonomy of hagfishes except for the presence, absence, or degree of pigmentation between bases and tips. No tabular comparison of lengths has previously appeared in print, perhaps due to the small numbers of specimens available. However, in this study a total of 2613 measurements of length of first nasal barbel, left side, provided material for comparison. Data in Table 6, first barbel length for 25-mm increments of total length, show significant differences in lengths within the five species treated.

Key to species of *Eptatretus* of the Pacific coast of North America

1a Prebranchial length usually less than branchial length, very rarely equal to or even slightly greater. Tail length always less than branchial length..... ..... ***E. mcconnaugheyi* n. sp.**

1b Prebranchial and tail lengths always greater than branchial length 2

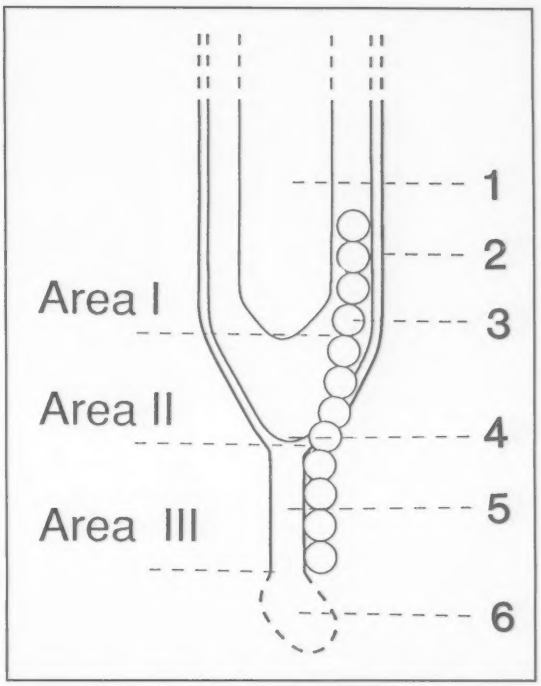

Figure 4
Sketch of branchial area, ventral view, of a hagfish (*Eptatretus*) delineating Areas I, II, and III, referred to in counts of gill pouches for each Area given in Table 8. (1) DM, posterior portion; (2) left branch of VA; (3) gill pouch; (4) point of branching of VA; (5) VA; (6) ventricle.

2a Prebranchial slime pores 7(4–10). Ventral finfold weakly developed, often vestigial or absent. Barbels small, not robust. Color dark purplish brown ..... ***E. deani***

2b Prebranchial slime pores 12–17. Ventral finfold variably well developed to absent. Barbels variably large to small. Color purplish to light or dark reddish brown 3

3a All barbels large, robust. Third barbel 49%(42–59%) of preocular length. Prebranchial slime pores 12–13(10–15). Branchial apertures 11(10–12). Ventral finfold very weakly developed, usually absent. Color dark purplish brown..... ***E. fritzi* n. sp.**

3b All barbels small, not robust. Third barbel 34%(31–37%) of preocular length. Prebranchial slime pores 13–17. Ventral finfold either prominent, vestigal or absent. Branchial apertures 10–14. Color dark brown to light reddish brown 4

4a Branchial apertures 12(10–14). Ventral finfold prominent, with wide pale margin. Color light reddish gray or light brown. Extensive piebaldness common ..... ***E. stoutii***

4b Branchial apertures 10(9–12). Ventral finfold vestigial or absent. Color dark reddish brown, not piebald ..... ***E. sinus* n. sp.**

Systematics

Eptatretus mcconnaugheyi new species

It is not feasible to attempt a meaningful synonymy for this new species, as it and *E. stoutii* are very similar and occur sympatrically off southern California. *Eptatretus stoutii* has long been extensively used in biochemical and physiological research. However, none of this research material has been examined by us, and no identification credited to competent ichthyologists. As *E. mcconnaugheyi* is not previously known, it is very likely to have formed a part of this research material, particularly from southern California.

Holotype SIO69-231E, female, 482 mm TL, taken at 32°32′0″N, 117°21′07″W, in a trap on bottom at 148 m, 11–12 April 1969.

Paratypes SIO69-228B, 14(185–400 mm TL), taken at 32°05.9′N, 117°04.4′W, 177 m, 10–11 March 1969; SIO71-114, 7(360–440 mm TL), taken at 28°21.0′N, 115°43.0′W, 689 m, 25–26 May 1971; SIO69-231E, 7(200–448 mm TL), taken with the holotype; SIO68-126, 5(355–409 mm TL), taken at 25°49′N, 110°51′W, 351 m, 25–26 January 1968; CAS 63203, 7(210–400 mm TL), taken at 32°31.8′N, 117°21.6′W, 145 m, 29 September 1972; LACM 44409-1, 6(195–430 mm TL), taken at 32°31.8′N, 117°21.1′W, 145 m, 29 September 1972; USNM 29630, 7(245–380 mm TL), taken at 32°31.8′N, 117°21.1′W, 145 m, 29 September 1972.

Additional material SIO56-9, 1(340), 42 m; SIO68-109, 1(390), 415 m; SIO68-11, 1(230), 177 m; SIO68-124, 1(249), 205 m; SIO68-125, 19(239–347), 278 m; SIO68-126, 5(355–409), 351 m; SIO68-127, 3(315–440), 238 m; SIO69-179, 2(235–376), 109 m; SIO69-181, 2 (141–312), 183 m; SIO69-225C, 1(392), 371 m; SIO69-228B, 14(195–406), 99 m; SIO69-228C, 1(433), 166 m; SIO69-231C, 1(372), 139 m.

Distribution *Eptatretus mcconnaugheyi* appears to consist of two disjunct populations: one from Santa Monica Bay, California, to the Cedros and San Benito Islands, Mexico, and one apparently restricted to the lower portion of the Gulf of California. These two populations appear to differ significantly ($P>0.001$) in numbers of trunk and total slime pores, the higher counts occurring in the southern California population.

Depths of capture range between 42 and 384 m off southern California and between 177 and 415 m in the Gulf of California. Collecting efforts between the Cedros and San Benito Islands and the mouth of the Gulf have failed to take the species.

Diagnosis Prebranchial length usually less than branchial length, rarely equal to or very rarely even slightly longer. Body moderately robust, deepest at midbody, its width about half its depth, increasingly laterally compressed toward tail. Tail length 13–16% of TL, its depth about half its length. Ventral finfold usually prominent, often low, with pale margin. Caudal finfold prominent, wide, the margin thin and pale. Three fused cusps (multicusp) on anterior, two fused cusps on posterior, set of cusps.

Etymology We take great pleasure in dedicating this new species to Ronald R. McConnaughey, friend and superb marine technician, who was instrumental in the development of capture gear and party to the collecting of many of the thousands of specimens of species examined by us.

Description Counts (Tables 2–8) and body proportions (Table 1) are given and compared with similar data for the other four species treated here. Body moderately robust, deepest at midbody, the width about half the depth, increasingly laterally compressed toward tail. Tail spatulate, its length about twice its depth, its ventral margin sloping downward below level of body. A thin, deep caudal finfold, with a narrow pale margin, extends from cloaca around end to about over cloaca dorsally. Ventral finfold low, usually entirely unpigmented. Head at eyespots about as deep as wide, narrowing to rostrum. Width of rostrum about half the width of head at eyespots. Eyespots rather prominent, of moderate size, the margins well defined. Oral surface short, sloping posteriorly at about 45° angle from the vertical. Barbels small, the distal thirds unpigmented. First barbel only slightly shorter than second, often equal to or slightly longer, averaging 64%(52–79%) of length of third, the second barbel averaging 70%(51–84%) of length of third. Length of first nasal barbel, left side, is given in Table 6 and compared with that of other species treated.

Head grooves Grooves present before and behind eyespots on each side of dorsal midline. Three to six grooves, each side, before eyespots lie in longitudinal rows, and two to four ventrad in transverse rows. One to eight grooves may occur behind eyespots. Most lie transversely, with none to three longitudinally, at sides. As many as 24 grooves may occur on one specimen.

Color a dark, reddish brown in life without pale spots or areas. Barbels pale on distal thirds.

Length of DM 27% (21–39%) of TL. DM width 68% (57–90%) of its depth. VA variable in length, averaging 11% (5–22%) of DM length. DM to VA 14% (5–26%) of DM length, and 1.4% (0.5–9%) of VA length. Number of GP in positions relative to DM and VA, Areas I, II, III, are given in Table 7, defined in Figure 4, and compared with similar data for the other four species discussed herein. Afferent duct of last GP, left side, always confluent with PCD.

Higher numbers of GA, left vs. right sides, may differ between the two populations (Table 8). Off southern California, the higher count is about equal for both sides at 4 and 5 each. In the Gulf population, the higher count is always on the left side.

Eggs The holotype contains 18 mature eggs, the largest 25.2 × 9.0 mm. The largest egg found in any female is 26 × 8 mm. The smallest female with eggs, most in round or slightly ovoid stages, is 267 mm TL. It may be that females of the Gulf population mature at a smaller size than do those from southern California. One, 267 mm TL, has eggs to 15.8 mm; one, 352 mm TL, has eggs to 20.8 mm; and one, 32 mm TL, has eggs to 17.6 mm. These figures contrast sharply with those of the southern California population, in which eggs ranging between 15 and 29 mm occur only in females of 400–508 mm TL. Perhaps these differences are an artifact of sampling or of developmental stages relative to both time and size, or to the relatively small number of specimens available (97).

All mature eggs of the holotype have fully developed anchor filaments (terminal hooks) with most free of encapsulating membrane (Fig. 3), and apparently ready for extrusion. This condition was rarely observed among the nearly 2400 specimens of all species of *Eptatretus* examined by us in the course of our studies. The eggs are linked by filaments in rows in a fashion similar to that shown by Dean (1989) and Jensen (1966).

The sex ratio is unbalanced. Of a total of 58 specimens for which sex could be reliably determined, 64% were female and 36% male.

Differentiation All body proportions and most counts for the two disjunct populations are very similar. However, significant differences ($P>0.001$) occur in numbers of trunk and total slime pores (Tables 3, 4), despite considerable overlap in values of thousandths of total length.

Discussion This species and *E. stoutii* appear to be closely related and occur sympatrically off southern California. However, the two are readily separable in that the prebranchial length of *E. mcconnaugheyi* is less, rarely even slightly longer, than the branchial length, and always greater in *E. stoutii*. Also, the numbers of prebranchial slime pores differ notably, 8–9 (6–11) in *E. mcconnaugheyi* and 13 (10–16) in *E. stoutii* (Table 2).

Eptatretus fritzi new species

Holotype SIO66-26, male, 550 mm TL, taken at 28°51′N, 118°14′W, in a trap on bottom at 512 m, 3–4 April 1966.

Paratypes SIO66-26, 30 (280–585 mm TL), taken with the holotype; CAS 63201, 15 (325–540 mm TL), taken with holotype; LACM 44407-1, 15 (375–495 mm TL), taken with the holotype; USNM 296318, 15 (350–570 mm TL), taken with the holotype; SIO63-177, 20 (324–522 mm TL), taken at 28°52′N, 118°14′W, 2743 m, 24 April 1963; SIO66-22, 36 (232–521 mm TL), taken at 29°06′N, 118°17′W, 402 m, 12 April 1966; SIO66-23, 195 (286–556 mm TL), taken at 28°54′N, 118°13′W, 444 m, 2–3 April 1966; SIO66-36, 2 (354–405 mm TL), taken at 29°30′N, 117°17′W, 512 m, 6–7 April 1966; SIO67-60, 120 (281–498 mm TL), taken at 29°09′N, 118°16′W, 832 m, 26–27 April 1966; SIO68-664, 2 (425–535 mm TL), 183 m, 15–16 November 1968; SIO72-294, 4 (207–541 mm TL), taken at 29°10′N, 118°16′W, 256 m, 12–13 April 1970.

Distribution Known only from the immediate vicinity of Guadalupe Island, Mexico. Depths of capture range between 182 and 2743 meters.

Diagnosis All barbels notably larger and more robust than on any other species of *Eptatretus* known to us (Table 6). Ventral finfold absent or vestigial, without pale margin. Prebranchial and tail lengths each greater than branchial length. Color a dark purplish-brown. Prebranchial slime pores 12 (10–15). Three fused cusps (multicusp) on anterior set of cusps, two fused cusps on posterior set.

Etymology We take great pleasure in dedicating this species to Frithjof (Fritz) Ohre, friend, willing, eager, and industrious volunteer on many of the expeditions on which all species treated here were taken, particularly those to Guadalupe Island.

Description Counts (Tables 2–8) and body proportions (Table 1) are given and compared with similar data for the other four species treated here. Body robust, deeper than wide, deepest at midbody, increasingly laterally compressed toward tail. Tail spatulate, its depth about half its length, its ventral outline not sloping downward from cloaca. Caudal finfold variably

thin to thick, beginning at cloaca and extending around tail to about over origin of cloaca, without pale margin. Ventral finfold usually absent, present in only 28 of 341 specimens (8.2%). When present it is intermittently and weakly developed along its length. It is thick, heavy, and without pale margin.

Head at eyespots about as deep as wide, narrowing to rostrum. Eyespots prominent, the margins irregular. Oral surface sloping posteriorly at about a 35° angle from the vertical. All barbels are notably longer and thicker in proportion to total length than on any other myxinid known to us (Table 6). First and second barbels about equal in length, the third averaging 49%(42–50%) of preocular length. First barbel as long or longer than width of nasal orifice when manually flattened (124%(100–203%)). First barbels average less than 50% of this width in all other species of *Eptatretus*.

Head grooves Grooves always present behind eyespots but occasionally absent before. Those behind average 5(3–10) in number and are arranged mostly in transverse rows with an occasional few grooves lying ventrad and longitudinally. Those before eyespots average 3(1–6) in number and lie longitudinally. Grooves behind eyespots originate very near the dorsal midline but do not cross. Those before eyespots are notably more distant from the midline.

Color Color a dark purple to black in most specimens, a chocolate brown in others, rarely showing pale spots. Notes by the senior author, party to the first and most subsequent captures, state, "a dark color." The chocolate color may be an artifact of preservation. GA, slime pore margins, and ventral finfold are without pale margins.

DM short, moderately robust, its length 27%(21–34%) of TL. DM width 13%(11–15%) of its length, its depth 73%(58–88%) of its width. VA length variable, 16%(8–42%) of DM length. DM to VA also variable, 15%(4–32%) of DM length and 90%(24–206%) of VA length. Numbers of GP in positions relative to DM and VA, Areas I, II, III, are given in Table 7, defined in Figure 4, and compared with similar data for the other four species treated here. Afferent duct of last GP, left side, always confluent with PCD.

Variation occurs in numbers of GA between left and right sides, the higher number always on the left side, 81 vs. 0 instances (Table 8).

Eggs The largest egg, 33.8 × 8.5 mm, occurred among 14 large eggs in a 386-mm TL female. No more than 16 and as few as 10 almost fully developed eggs were found in any female. No egg had free anchor filaments, but occasionally they were visible through the encapsulating membranes.

The sex ratio is unbalanced. Of a total of 358 specimens for which sex could be reliably determined, 60% are female and 40% male.

Discussion This species and *E. deani* occur sympatrically near Guadalupe Island, Mexico. Both were taken in the same trap on two occasions. They are similar in coloration, being very dark brown to purplish-black, but *E. fritzi* seems much less prone to piebaldness than *E. deani* as very few pale spots were noted. Primary differences are that the barbels of *E. fritzi* are much longer and more robust than those of *E. deani* (Table 6), and that it has more prebranchial pores, 12 (10–15) vs. 7(4–10). Also, *E. fritzi* usually has no ventral finfold (313 of 341 specimens, 91.8%), whereas in *E. deani* this finfold is usually present (863 of 892 specimens, 96.6%), although rather weakly developed.

Eptatretus sinus new species

Holotype SIO68-108, female 307 mm TL, taken at 25°49′N, 110°44′W, in a trap on bottom at 708 m, 22–23 January 1968.

Paratypes SIO68-108, 31(230–425 mm TL), taken with the holotype; SIO68-94, 29(129–346 mm TL), taken at 29°20′N, 113°10′W, 263 and 283 m, 20 January 1968; SIO68-100, 60(267–464 mm TL), taken at 29°00′N, 113°25′W, 467 m, 20–21 January 1968; CAS 63202, 15(270–400 mm TL), taken at 25°49′N, 110°44′W, 708 m, 22–23 January 1968; LACM 44408-1, 14 (270–400 mm TL), taken at 25°49′N, 110°44′W, 708 m, 22–23 January 1968; USNM 296319, 15(275–420 mm TL), taken at 25°49′N, 110°44′W, 708 m, 22–23 January 1968.

Additional material SIO68-97, 7(223–308), 881 m; SIO68-98, 17(276–338), 881 m; SIO68-99, 11(263–420), 668 m; SIO68-101, 16(264–355), 198 m; SIO69-201, 1 (190), 1454 m; SIO69-203, 11(381–630), 759 m; SIO69-206, 54(363–430), 768 m; SIO69-207, 57(259–404), 475 m.

Distribution Known only from the midriff area of the Gulf of California, Mexico, between about 28° and 30°N latitudes. Depths of capture range between 198 and 1330 meters.

Diagnosis Prebranchial length greater than branchial length. Tail length usually greater than branchial length, occasionally equal to or less. Ventral finfold low, unpigmented, occasionally absent. Barbels usually unpigmented, except rarely at bases. Three fused cusps (multicusp) on anterior, two fused cusps on posterior, sets of cusps.

Etymology From the Latin "sinus," meaning gulf, by reason of its apparent restriction to the midriff area of the Gulf of California, Mexico.

Description Counts (Tables 2–8) and body proportions (Table 1) are given and compared with similar data for the other four species treated here.

Body robust, deepest at midbody, deeper than wide, increasingly laterally compressed toward tail. Tail spatulate, its depth about half its length, its ventral outline not sloping downward from cloaca. Caudal finfold thickened ventrally, thinner around tail, ending dorsally over cloacal origin. Ventral finfold usually present, low, unpigmented. It is absent on 10% of 363 specimens.

Head at eyespots as deep as wide, the oral surface sloping posteriorly at about 35° from the vertical. Eyespots prominent, the margins well defined. Barbels short, unpigmented except rarely at bases. Second barbel usually longer than first but occasionally shorter or of equal length. First and second barbels respectively 60% and 64% of third barbel. Length of first nasal barbel is given in Table 6 and compared with that of other species treated.

Head grooves Grooves present before and behind eyespots, each side. One to five grooves occur behind eyespots, most lying transversely, but a few lying longitudinally at side of head. One to four grooves lie before eyespots in longitudinal rows. Occasionally no grooves occur before eyespots.

Color Color reddish-brown, without pale markings or spotting. GA, PCD, and an occasional slime pore have narrow pale margins.

Length of DM 24%(21–29%) of TL. DM width 14% (12–17%) of its length, its depth 65%(54–86%) of its width. DM to VA 16%(15–26%) of DM length. VA length 25%(17–39%) of DM length. VA length variable, averaging 66%(22–127%) of distance from DM to VA. Numbers of GP in position relative to DM and VA, Areas I, II, III, are given in Table 7, defined in Figure 4, and compared with similar data for the other four species treated here. Afferent duct of last GA, left side, always confluent with PCD.

Variation in numbers of GA occurs between left and right sides, with higher numbers predominating on the left, 65(15%) vs. 8(2%), *N* 444 (Table 8).

Eggs The holotype, 370 mm TL, contains many small eggs, to about 4 mm. The largest egg found (among 21 large ones) was 32 × 7.5 mm in a female of 371 mm TL. The most eggs found was 37 (18 × 5 mm) in a female of 420 mm TL. Eggs (28) to 21 mm were found in a female of 372 mm TL, and to 23 mm in one of 335 mm TL. Apparently, *E. sinus* matures at a short total length, as a male of 130 mm and a female of 142 mm were noted. These are surprisingly small sizes, for in other species, these total lengths are distinctly juvenile, and the sex determinable only under very high magnification, if at all. Encapsulated anchor filaments are visible on eggs of 20 mm length.

The sex ratio of *E. sinus* is unbalanced. Of a total 424 specimens for which sex was reliably determined, 65% are female, 35% male.

Eptatretus deani (Evermann and Goldsborough 1907)

Synonymy

Polistotrema deani Evermann and Goldsborough 1907: 221–222, 225–226, fig. 1 (original description; compared with *Polistotrema stoutii*; Albatross Station 4235, Spacious Bay, Cleveland Peninsula, 130–193 fathoms, and Albatross Station 4238, Nose Point, Behm Canal, southeastern Alaska, 229–231 fathoms); Wilimovsky 1954a: 3, and 1954b: 281 (SE Alaska to California), 1958: 18 (compared with *P. stoutii*; SE Alaska to California); Barham et al. 1967: 780, fig. 7 (shown associated with *Anoplopoma fimbria*, Trieste Dive 105; 1060 m in San Diego Trough) [presumptive].

Polistotrema curtiss-jamesi Townsend and Nichols, 1925: 4–5, 18, 20, fig. 1 (original description; compared with *P. stoutii*; south of Monterey to Santa Barbara I.: 440–585 fathoms; Albatross Stations 5695, 5696, 5697, 5698; type locality Station 5697, 585 fathoms).

Heptatretus deani Regan, 1912: 534–535 (comparisons; synonymy; references; diagnosis; Alaska).

Bdellostoma deani, Adam and Strahan 1963; 6 (11–12 gills; length to 620 mm; Alaska).

Eptatretus deani, Day and Pearcy 1968: 2668, 2771 (listed; about 1200 meters off Oregon); Bourne and McAllister 1969: 3246–3248, fig. 1 (first British Columbia records, 54°47′N, 130°58′30″W at 90–250 fathoms: 48°53′N, 126°40′W at 373 m: description); Kukowski 1972: 7, 24 (Monterey Bay; references); Miller and Lea 1972: 32 (Cedros and Guadalupe Is., Baja California to SE Alaska: length to 20 inches; depth 1560–3500 feet; common in deep water, uniform purplish black); Fitch 1973; 815 (off Eureka, California, 565–585 m); Hart 1973: 10, 16–18, fig. 1 (first description for Canada; comparisons in key; description; geographical and bathymetric distributions; references); Gates and Frey 1974: 60 (vernacular, California): Smith and Hessler 1974; 72–73 (14 miles off San Diego; depth 1230 m; respiration rate measured *in situ*; a dominant species in San Diego Trough); Jespersen 1975: 189–190, 195, 197,

fig. 15 (spermiogenesis; southern California off San Clemente I. at about 1280 m; off Los Coronados I. at about 1097 m; Theisen 1976: 167–173, figs. 2. 4. 7. 10 (microstructure of olfactory system; southern California; 1097 m.

Holotype USNM 57820, sex not determined, "21" inches (about 535 mm TL), taken near Yes Bay, Behm Canal, Cleveland Peninsula, southeastern Alaska, easterly of Ketchikan, about 55°55′N, 131°55′W, by dredge at 419–423 m (Albatross Station 4238), 8 July 1903.

Paratypes USNM 61162, two: one a female, in rotting condition, taken at Albatross Station 4229 and 4235, Behm Canal, southeastern Alaska, Nose Point, near the holotype, by dredge at 419–423 m, 16 July 1903. (The type specimens were examined by Carl L. Hubbs at USNM, 25 February 1972.)

Additional material SIO59-47, 6(359–458), 823 m; SIO60-540, 1(484), 1920 m; SIO63-177, 20(286–457), 2743 m; SIO63-868, 21(345–498), 107 m; SIO64-281, 1(451), 587 m; SIO64-496, 5(374–455), 475 m; SIO64-497, 26(335–445), 512 m; SIO64-498, 37(291–441), 616 m; SIO64-499, 38(294–473), 960 m; SIO65-499, 54 (321–521), 933 m; SIO65-465, 19(370–554), 1302 m; SIO66-27, 2(148–455), 1252 m; SIO66-36, 130(233–509), 512 m; SIO66-535, 21(377–453), 1013 m; SIO66-537, 1(417), 1244 m; SIO66-551, 2(390–401), 1156 m; SIO67-64, 20(380–510), 980 m; SIO67-109, 52(312–523), 1024 m; SIO67-110, 1(369), 1445 m; SIO67-118, 51(288–467), 732 m; SIO68-427, 5(396–470), 1840 m; SIO68-428, 6(320–481), 800 m; SIO69-225F, 38(342–429), 633 m; SIO69-227B, 26(288–495), 744 m; SIO69-288D, 56(182–423), 609 m; SIO71-103, 4(401–484), 1373 m; SIO71-7, 42(280–484), 1244 m.

The following collections, with incomplete data were taken between British Columbia and northern California: OSUO 3869, 3(267–450), OSUO 3870, 2(385–415), OSUO 3871, 2(404–447), BCPM 46-15, 1(366), BCPM 72-9, 4(402–475), BCPM 72-10, 1(460), CAS 10877, 1(390), CAS 26633, 2(318–365), CAS 20404, 1(395), Albatross Station 3126, 1(317), 378 m; UW 00379, 1(440), 155 m; UW 18148, 1(391), 595 m; UW 18149, 1(383), 1098 m; UW 18151, 1(405), 1190 m; UW 18152, 7(370–445), 1190 m; UW 18153, 2(402–466), 932 m; UW 18154, 1(354), 183 m; UW 18155, 6(376–433), 1190 m; UW 18157, 5(400–440), 732 m; UW 18158, 12(342–459), 824 m; UW 18159, 2(343–375), 732 m; UW 19095, 3(421–440), UW 19127, 2(414–444), UW 19206, 1(320), UW 19310, 6(382–479).

Distribution Southeastern Alaska to near Guadalupe Island, Mexico. Despite this extensive range of about 2600 miles, no significant variation in counts or measurements with latitude was demonstrated.

Diagnosis Prebranchial slime pores 7(4–10). Prebranchial length usually greater than branchial length, rarely equal to or less. Tail length variably equal to, or slightly less or greater than branchial length. Color a purplish-black, with occasional pale spots and areas. Anterior part of head often pale. Three fused cusps (multicusp) on anterior set of cusps, two fused cusps on posterior set.

Description Counts (Tables 2–8) and body proportions (Table 1) are given and compared with similar data for the other four species treated here.

Body robust, deeper than wide at midbody, progressively laterally compressed toward tail. Prebranchial slime pores 7(4–10). Branchial apertures 11(10–12). Prebranchial length usually greater than branchial length, rarely equal to or less. Tail length greater than branchial length in 45%, equal-to in 30%, and less-than in 26% of 441 specimens. Ventral finfold weakly developed, occasionally absent, without pale margin. Tail spatulate, its ventral surface sloping downward at a slight angle from the ventral body line. Head wider than deep. First barbels usually shorter than second, occasionally equal to or slightly longer; the first about 58% of length of third barbel, the third about 70% of preocular length. Eyespots prominent, variable in size, usually with irregular margins. Length of first nasal barbel is given in Table 6 and compared with that of other species treated.

Head grooves Of 104 specimens selected for mucus-free condition, 18 (17%) had no grooves. Of those having grooves before eyespots, 45% had them on both sides, about 6% had them on either the right or left side only. Grooves occur on both sides behind eyespots in 80%, on the left only in 8%, and on the right side only in 12% of the 104 specimens.

Color Color usually a purplish-black or very dark brown. Specimens with a brownish base color show variable amounts of pale spots and patches (piebaldness) that range from slight to considerable. An occasional specimen has a pale head from rostrum to first few prebranchial slime pores. Most heads are pale near tip of rostrum. On pale heads, the barbels usually are unpigmented. Ventral and caudal finfolds without pale margin except when spotted in piebald specimens. Gill apertures and slime pores with narrow pale margins. Cloacal margins with rather wide pale areas.

Variation occurs in numbers of GA between left and right sides with higher numbers predominating on the left, 125 (11%) vs. 21 (2%) on the right side in 1145 counts (Table 8).

DM length 24% (20–26%) of TL. Width of DM 15% (13–18%) of its length, its depth 64% (54–80%) of its width. DM to VA 9% (0–15%) of DM length. VA length 31% (23–36%) of DM length. Numbers of GP in positions relative to DM and VA, Areas I, II, III, are given in Table 7, defined in Figure 4, and compared with similar data for the other four species treated herein. Afferent duct of last GA, left side, always confluent with PCD.

Eggs Mature eggs large, usually distinctly curved. The largest egg found measured 52.3 × 10.5 mm and was among 14 large eggs in a 500-mm TL female. Apparently very few eggs mature at one time from the many hundreds of tiny, round to slightly ovoid eggs normally present. No more than 15 nor fewer than 8 large eggs (30 mm and longer) were present in any female. Anchor filaments were visible on all eggs of 35 mm length or more, but were still encapsulated.

The sex ratio of *E. deani* is notably unbalanced. Of a total of 480 specimens, 74% were female, 26% male. The smallest female noted was 249 mm TL, the smallest male 255 mm TL.

Eptatretus stoutii (Lockington 1878)

Synonymy The following synonymy includes only those references arbitrarily considered by us to have taxonomic, behavioral, or distributional value and not mere usage of the name. About 120 references using the name *stouti* or *stoutii* pertain only to biochemical and/or physiological studies that serve no apparent taxonomic purpose and are not included.

Bdellostoma stoutii Lockington, 1878:792–793 (original description; compared with *B. polytrema*; mouth of Eel River, Humboldt County, California); Jordan and Gilbert 1883:6 (brief description, after Lockington; coast of California; not rare).

Bdellostoma stouti, Dean 1899:223–276 (embryonic development of larvae and eggs).

Bdellostoma dombeyi, Jordan and Gilbert 1883:57 (in part; characters and feeding habits; California); Worthington 1905:625–663 (description, behavior in aquaria; habitat in Monterey Bay; counts of gill openings; feeding; eggs); Ayers and Worthington 1907: 327–336 (figures and description, lateral lines found only on head).

Homea stoutii, Dean 1903:295–298 (partial albinism in anterior portion), 1904: 6. 7. 16, 18, 20 (seasonal spawning; largest are females; California).

Heptatretus stouti, Regan 1912:534–535 (synonymy; comparisons; diagnosis; California).

Eptatretus stouti, Starks and Morris 1907:161 (common in deep water off San Diego; north to Cape Flattery; abundant in Monterey Bay); Strahan 1963:22 (behavior and attitudes in aquaria); Linthicum 1971: 17–22 (immunological study; tying itself in knots to remove slime; slime production, teeth); Kukowski 1972:24, 37, 43 (Monterey Bay and Elkhorn Slough; references), 1973:7, 19, 22–23 (Monterey Bay; occurrence data; recurrent groupings); Anonymous 1973: 68 (observed at camera station at 306 m, SW of White's Point, southern California); Allen 1976:95 (only species not taken in otter trawl or by setline in Santa Monica Bay, southern California; has been so collected elsewhere); Downing et al. 1981:326–328 (description and figures of mucus thread cells in slime glands); Fernholm 1985:113–122 (in part; no ciliated cells or innervation or electroreceptory capacity found in lateral lines).

Polistotrema stouti, Clemens and Wilby 1946:9 (characters; white margin on ventral finfold; reaches 25 inches; species attacked; attachment of eggs; W coast, Vancouver I.).

Polistotrema stoutii, Fowler 1908:461 (Pacific Grove on Monterey Bay, California; gill opening counts for 8 specimens); Clemens and Wilby 1961:18, 49–50 (description; history on British Columbia west coast; eggs; southern California to SE Alaska; in part); McInerney and Evans 1970:966–968 (habitat characteristics; Mayne Bay in Barkley Sound, Vancouver I.); Sasaki 1972:283 (Queen Charlotte Sound, Vancouver I.; rare).

Dodecatrema stoutii, Fowler 1947:3 (proposed new name to replace *Bdellostoma*).

Eptatretus stoutii, Jensen 1959:798 (albino and piebald variants; ratio to normal; habitat; abundance in southern California; submarine canyons tributary to San Diego Trough; 210 fathoms), 1966:82–90 (habits; description and figures of the four hearts; functions); Taylor 1967:181–187 (chromosome numbers; probably supernumeraries; Alaska to Baja California; habitat; 60–1800 feet); Day and Pearcy 1968:2668 (depth distribution off Oregon); Bourne and McAlister 1969:3248 (compared with *E. deani*); Miller and Lea 1972:32 (Pt. San Pablo, Baja California, to SE Alaska; length to 25 inches; depth range 30–2400 feet; description); Hart 1973:16, 18–19, 53 (comparisons in key; description; common; geographical and bathymetric distribution in and off Barkley Sound; probably quite generally distributed in British Columbia; Alaska records not confirmed in recent reviews; references; egg cases); Smith and Hessler 1974:72–73 (*in situ* respiration rate significantly greater than that of *E. deani*); Anonymous 1974:50 (observed only during day at baited camera off Palos Verdes, California); Fernholm 1975:201–203 (structure and deposition of eggs compared with that of *E. burgeri*; *Bdellostoma dombeyi* of Worthington referrable to *E. stoutii*); Jespersen 1975:189–198

(spermiogenesis; offshore in 45.7 and 53.0 m); Knaggs et al. 1975:56–57 (taken off central Baja California; southern range extended from Cedros I. to Pt. San Pablo); McMillan and Wisner 1984:255 (lateral line described and figured); Wisner and McMillan 1988:231 (the term "head grooves" suggested to replace that for lateral lines.

Neotype SIO68-426, male, 530 mm TL, taken about 2 miles southwest of the whistler buoy at entrance to Humboldt Bay, California, in a trap on bottom at 38–44 m, on 27 August 1963.

Additional material, northernmost collections SIO 68-426, 34(291–527), taken with the neotype. BCPM 60-1, 2(474–580), taken at about 49°33′N, 126°38′W, outside Nootka Bay, Vancouver I.; no other data; BCPM50-3, 2(192–420), taken off west coast of Vancouver I.; no other data; BCPM98-2, 1(506), taken off west coast of Vancouver I.; no other data; UW-15869, 4(144–400), taken at 48°51.8′N, 124°35.8′W, in Strait of Juan de Fuca, in a trawl; depth not recorded; 27 March 1956; UW-18161, 6(437–512), taken "8 mi out" from Depoe Bay, Oregon at 79 m; method of capture not recorded, 30 August 1964; CAS 19191, 1(403), taken at Holmes Harbor, Puget Sound; no other data; OSU-OTB-180, 1(435), taken at 44°43.5′N, 124°18.1′ W, in a bottom trawl at 96 m, 24 July 1967.

Twelve collections in the California Academy of Sciences, comprising one or two specimens each, and with very incomplete or absent capture data, were taken between Cape Mendocino and San Diego, California (CAS 6832, 7353, 11115, 12751, 12881, 20290, 26491, "Acc. 1954:XI:23," IU 1006, 1069, 1086, 1613 (the IU collections are now at CAS). Similarly, three collections (MCZ 28802, 28803, and 32782), totaling five specimens, with very limited data, were taken in Monterey Bay, California.

Material was taken in 1963 by David Jensen, then of Scripps, in collaboration with the University of Washington Atomic Energy Program. Most specimens were sacrificed to that program. A total of six collections were made between Cape Disappointment, at mouth of Columbia River, off Depoe Bay, Oregon, off Humboldt Bay, and Fort Bragg, California. Numbers of specimens ranged between 6 and 152, and were taken at depths of 38–132 m in bottom traps.

More than 40 collections, comprising nearly 1500 specimens, taken in the southern California area (Pt. Conception to Islas Todos Santos, Baja California, Mexico) were used for certain counts but are not listed among the study material. In addition, hundreds of specimens in the Scripps Marine Vertebrate Collection taken off San Diego were examined for certain characters only and are not listed. However, all collections from outside the Southern California area are listed.

Southernmost collections SIO59-92, 1(345), 28°23′ N, 115°21′W, 280 m; SIO62-91, 3(164–207), 28°11′N, 115°23′W; SIO64-951, 1(363), 31°08′N, 116°35′W, 137 m; SIO71-114, 30(300–465), 28°21′N, 115°43′W, 384 m; SIO71-121, 7(283–384), 28°18′N, 115°29′W, 311–330 m; SIO71-126, 83(195–460), 30°22′N, 116°07′W, 201 m; SIO73-373, 2(320–395), 28°50′N, 114°48′W, 92–95 m.

Distribution Nootka Bay, west side of Vancouver Island, British Columbia, Canada, to Pt. San Pablo, Baja California (about 27°14′N, 114°30′W). Although *E. stoutii* has been reported from southeastern Alaska, we have found no valid records of capture north of Nootka Bay (about 49°33′N, 126°38′W). Despite this extensive range of about 2200 miles, no significant variation in counts or measurements with latitude was demonstrated.

Carl L. Hubbs, at USNM, 28 June 1972 (personal notes), examined collections from southeastern Alaska, labeled as *E. stoutii*, and found them to be either misidentified or with the capture data indicating localities far from Alaska, as follows: USNM 53963, listed as from southeastern Alaska, but with coordinates indicating the vicinity of Monterey, California; USNM 53964, listed as from Alaska, but with coordinates given as 33°08′N, 118°40′W, the vicinity of Santa Barbara, California. Hubbs recorded this specimen as *E. deani* "without question;" USNM 73737, Albatross Station 3077, east of Sitka, Alaska, labeled as *E. stoutii* but referrable to *E. deani*, based on the skin being jet black and eggs to 38 mm length—a length much greater than found in *E. stoutii* (28 mm); in addition, a collection, UW 02738, four, 332–390 mm TL, was recorded simply as "S.E. Alaska; International Fish Commission, 1931."

Depths of capture range between 16 m off the San Onofre Nuclear Power Plant, near San Clemente, southern California, and 633 m at 31°47′N, 116°50′W, south of Ensenada, Baja California, Mexico.

Latitude may be of limited significance in depths of capture (habitat), as the farthest-north least depth is 44 m, off Humboldt Bay, and the farthest south the 16 m capture off the San Onofre Nuclear Power Plant. The species has been taken by scuba divers between 18 and 21 m near La Jolla, California.

Diagnosis Body slender, only slightly deeper than wide. Prebranchial length greater than branchial length. Branchial apertures 12(10–14). Ventral finfold prominent, the distal margin pale. Eyespots small, prominent, the margins well defined. Color a light brown with pale spotting and small blotches common.

Three fused cusps (multicusp) on upper and two fused cusps on lower sets of cusps.

Description Counts (Tables 2–8) and body proportions (Table 1) are given and compared with similar data for the other four species treated herein.

Body slender, only slightly deeper than wide, progressively laterally flattened toward tail. Tail spatulate, its ventral profile not slanting downward, but lying on a straight line with ventral profile of body, its depth 43% (30–56%) of its length. A thin, well developed, pale-margined finfold extends from cloaca around tip of tail, ending about over cloaca. Tail length usually greater than branchial length, but is equal-to in 12% and less-than in 8% of 421 specimens. Ventral finfold prominent, with pale distal margin. Head at eye spots about as deep as wide, narrowing toward rostrum. Eyespots small, with distinct margins. Barbels small, usually without pale tips. Second barbel usually longer than first, the first shorter than second in 41%, about equal to in 51%, and longer than second in 7% of 315 specimens. First barbel 51% (41–84%), the second 64% (49–98%) of third barbel. Length of first nasal barbel is given in Table 6 and compared with that of other species treated.

Variation occurs in numbers of GA, left and right sides, with higher numbers predominating on the left, 167 (11%) vs. 56 (4%), N-1554 (Table 8).

Head grooves Grooves present above and below eyespots. Two to four (rarely five) grooves lie above eyespots in lines nearly parallel to the longitudinal axis of the body. Grooves below eyespots are arranged in two groups; 2–5 grooves lie transversely, and from 0–3 lie alongside laterad to and nearly parallel with the longitudinal axis. No grooves cross the dorsal midline.

Color Color ranges between a light to purplish-gray to light brown, with occasional pinkish overtones. Pale spots and blotches (piebaldness) are common. Complete albinism and piebaldness was reported by Jensen (1959:798, figs. 1, 2). Dean (1903:295–296, fig. 1) descriped and figured a specimen with large pale areas on head and anterior ventral surface.

DM short, moderately robust, its length 25% (22–28%) of TL, its width 12% (11–13%) of DM length, its depth 74% (64–77%) of its width. Distance from tip of DM to branching of VA 14% (8–20%) of DM length, and that distance is 42% (25–72%) of VA length. VA length 32% (22–40%) of DM length. Numbers of GP in positions relative to DM and VA, Areas I, II, III, are given in Table 7, defined in Figure 4, and compared with similar data for the other four species treated here. Afferent duct of last GA, left side, always confluent with PCD.

Eggs The largest egg found measured 28.6 × 7.5 mm, in a female of 435 mm TL. Well developed eggs with anchor filaments are visible but encapsulated. The number of almost fully developed eggs (20 mm or longer) varies from 11 (23 × 7 mm) in a 330-mm TL female to 48 (20 × 6 mm) in one of 515 mm TL. Neither specimen had been opened prior to our examination.

Sex was determinable in a female of 179 mm TL (the eggs tiny) and in a male of 200 mm TL.

The sex ratio of the study material is essentially equal. Of a total of 870 specimens for which sex was reliably determined, 49% were female, 51% male. This ratio contrasts notably with other species described herein, in which females dominated by 60–74%. The maximum size of each sex appears to be equal, the largest male measuring 550 mm TL, the largest female 515 mm TL. Four large females ranged between 491 and 500 mm TL, the next largest 475 mm TL.

Discussion Lockington (1878:792–793) very briefly described *Bdellostoma stoutii* as, "Eleven gill openings on each side; ten teeth in the anterior and nine in the posterior series. 15½″ long. Eel River, Humboldt County."

There is no doubt that the specimen represented a hagfish, but Lockington's subsequent statement indicates that perhaps he confused it with a species of lamprey, possibly *Lampetra tridentata*, as he stated, "It is rather singular that this fish, which is abundant in Eel River and is sold for food, and also occurs in this harbor, should have hitherto escaped notice. I believe it to be the only species of its genus hitherto found on the Pacific coast of North America; and it differs from *Bdellostoma polytrema*, a species which occurs along the coast of Chile, both in the number of its gill openings and that of the teeth, *B. polytrema* having fourteen of the former and twelve of the latter in each series."

There can be no serious question as to the pertinence of the name *stoutii* to this species, although the diagnosis is extremely short and Lockington ascribed the species primarily to Eel River, indicating it as abundant there. But he added, "also occurs in this harbor," meaning, presumably, San Francisco Bay, since there is no harbor at the mouth of Eel River, but only an estuarine embayment.

Perhaps the specimen was sent from near the mouth of Eel River, almost certainly from central or northern California. We maintain the name *stoutii* because it is the only other species of the genus from the area fitting the description. *Eptatretus deani* is a deep purplish-black in color, not light brown. It generally occurs at much greater depths, and it is unlikely that a fisherman would have taken *E. deani* in the 1870s because of this greater depth of habitat. Unfortunately, Lockington did not state the numbers of prebran-

chial pores, which, aside from color, is an important character separating the two species.

Lockington did not designate his specimen as a holotype or state that it was deposited anywhere. If deposited, the most likely place would have been the California Academy of Sciences. W.E. Eschmeyer (Calif. Acad. Sci., San Francisco, pers. commun.) has informed us that Lockington's specimen is not now at the Academy, and stated that it and any record of it may have been destroyed in the San Francisco earthquake and fire.

Therefore, in view of the possible confusion of *E. stoutii* with *E. mcconnaugheyi*, especially off southern California, we designate as neotype of *Eptatretus stoutii*, SIO68-426, a male, 530 mm TL, taken near the whistler buoy at entrance of Humboldt Bay, California. This locality is about 8 miles northerly from the mouth of Eel River, the type locality of Lockington's *Bdellostoma stoutii*.

Discussion

The relationship of the five species treated above superficially appear to be close. We are aware of the speculative and debatable nature of intraspecific variation, and that any proposed new species may be considered a variant of a similar-appearing, sympatric known species.

Thus, it may be argued that *E. deani* and *E. fritzi* are mere variants, due primarily to their very dark coloration, much darker than in any of the other species treated, and due perhaps to their sympatric occurrence in the presently restricted range of *E. fritzi* near Guadalupe Island, Mexico. However, the virtually non-overlapping numbers of prebranchial slime pores, 7(4–10) in *E. deani* vs. 12–13(10–15) in *E. fritzi* (Table 2), alone are adequate for specific separation. In addition, the very large barbels of *E. fritzi* do not occur in *E. deani* (Table 6) of sympatric occurrence or in any portion of the nearly 2600 miles of its total range.

The superficial similarity of *E. stoutii* and the sympatric *E. mcconnaughtyi* also invites speculation as to being mere variants. However, the notable and non-overlapping difference in respective prebranchial lengths alone distinguishes between the two species (Table 1). Also, the numbers of prebranchial slime pores differ significantly, with minor overlap (Table 2).

Similary, *E. stoutii* and *E. sinus* are alike in most counts and proportions, but the very prominent ventral finfold of *E. stoutii* does not occur in *E. sinus*, where it is absent or vestigial. Also, when fresh material of each is compared, the much darker reddish-brown of *E. sinus* contrasts sharply with the much lighter gray-reddish brown of *E. stoutii*.

All the above principal characters differentiating the five species are constant, often non-overlapping, and show little or no variation within species.

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Table 1

Averages and ranges (in thousandths of total length) of selected body proportions for five species of hagfishes (genus *Eptatretus*) from the Pacific coast of North America. Values for type specimens are given first and followed in parentheses by ranges in values for all material.

Species	Average (range of values)				
	E. mcconnaugheyi	*E. fritzi*	*E. sinus*	*E. deani*	*E. stoutii*
N (Size range in mm)	91 (147–470)	233 (207–592)	458 (129–481)	460 (130–523)	520 (179–468)
Preocular length	62 (45–74)	54 (48–82)	52 (41–82) *	61 (42–89)	53 (40–77)
Prebranchial length	153 (147–181)	198 (176–245)	226 (197–278)	175 (144–204)	240 (187–253)
Branchial length	200 (155–216)	140 (115–158)	113 (92–172)	155 (127–182)	138 (115–142)
Trunk length	532 (482–557)	499 (462–556)	501 (450–540)	517 (480–555)	509 (470–535)
Tail length	130 (122–161)	158 (132–181)	151 (102–174)	151 (126–192)	134 (104–178)
Tail depth	72 (60–88)	65 (58–92)	78 (48–90)	80 (52–103)	55 (45–83)
Body depth with finfold	91 (61–98)	No finfold	67 (49–104)*	78 (47–105)	62 (50–97)
Body depth without finfold	89 (55–90)	63 (53–102)	58 (46–101)*	72 (45–105)	51 (41–90)
Body depth at cloaca	53 (47–71)	56 (45–72)	61 (39–86) *	63 (38–85)	53 (38–79)

*330 specimens measured.

Table 2

Numbers of gill pouches, prebranchial, branchial, and tail slime pores for five species of hagfishes (genus *Eptatretus*) from the Pacific coast of North America. Values, left side, for type specimens are indicated by an asterisk.

	Gill pouches															
	9	10	11	12	13	14								*N*	$\bar{X}$	δ
E. mcconnaugheyi				28	67*	2								97	12.73	0.487
E. fritzi		31	261*	64										356	11.09	0.508
E. sinus	77	248*	103	7										435	10.09	0.685
E. deani		21	536	43										600	11.04	0.325
E. stoutii		2	173	691*	63	2								931	11.88	0.507
	Prebranchial slime pores															
	4	5	6	7	8	9	10	11	12	13	14	15	16	17	*N*	$\bar{X}$	δ
E. mcconnaugheyi			1	5	27	50*	11	2							96	8.74	0.845
E. fritzi							3	40*	123	118	31	3			318	12.45	0.898
E. sinus							3	27	85	142*	117	44	14	3	435	13.26	1.231
E. deani	1	7	90	275	197	23	7								600	7.26	0.854
E. stoutii							2	29	142	366	315*	59	7		920	13.27	0.946
	Branchial slime pores															
	8	9	10	11	12	13	14	15	16						*N*	$\bar{X}$	δ
E. mcconnaugheyi				15	52	16*	5	2	2						92	12.27	1.012
E. fritzi		14	233	105*	4										556	10.28	0.549
E. sinus	72	246*	107	10											435	9.13	0.698
E. deani		16	425	125	30	4									600	10.30	0.636
E. stoutii		3	151	587	80*	1	1								823	10.91	0.551
	Tail slime pores															
	7	8	9	10	11	12	13	14	15						*N*	$\bar{X}$	δ
E. mcconnaugheyi		2		21	44*	22	8								97	11.13	0.915
E. fritzi		2		19	87	149	80*	18	1						356	11.96	0.999
E. sinus	2	28	130	168	76*	22	7	2							435	9.90	1.088
E. deani			7	128	224	188	47	5	1						600	11.27	0.958
E. stoutii		4	64	239*	357	125	22	2							813	10.75	0.935

Table 3

Numbers of trunk slime pores for five species of hagfishes (genus *Eptatretus*) from the Pacific coast of North America. Values, left side, for type specimens are indicated by an asterisk.

	Trunk slime pores																		
	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	*N*	$\bar{X}$	$\acute{o}$
E. mcconnaugheyi																			
Southern California								8	7	6	13	13*	8	3	2		60	46.03	1.871
Gulf of California				1	2	3	4	11	11	3	2						37	43.08	1.566
E. fritzi					2	3	15	38	85	112	67*	24	9	1			356	44.77	1.413
E. sinus	1	4	10	35	64	102	86*	65	40	12	7	7	1	1			435	41.67	1.943
E. deani				1	2	6	38	87	137	152	99	51	22	5			600	44.70	1.601
E. stoutii				1	8	38	96	154	196*	154	110	41	13	5	2	1	819	44.12	1.726

Table 4

Numbers of total slime pores for five species of hagfishes (genus *Eptatretus*) from the Pacific coast of North America. Values, left side, for type specimens are indicated by an asterisk.

Total slime pores	*E. mcconnaugheyi*		*E. fritzi*	*E. sinus*	*E. deani*	*E. stoutii*
	Southern California	Gulf of California				
66				1		
67		2		2	2	
68				9	5	
69				11	16	
70		1		16	26	
71		2		39	48	1
72	2	5		57	100	1
73	2	8		53	111	1
74	5	11	1	63	98	11
75	3	3	6	60*	78	26
76	2	1	14	59	63	61
77	11	1	38	21	34	107
78	12	2	50	16	16	142
79	9	1	87	12	2	141
80	6*		71	9	1	116*
81	2		46*	4		100
82	4		23	3		60
83	1		10			29
84	1		8			12
85			2			7
86						3
87						
88						1
N	60	37	356	435	600	819
$\bar{X}$	77.80	73.43	79.36	73.98	75.91	79.03
$\acute{o}$	2.650	2.444	1.909	2.796	2.186	2.280

Table 5

Numbers of anterior and posterior unicusps, and total cusps, for five species of hagfishes (genus *Eptatretus*) from the Pacific coast of North America. Values, left side, for type specimens are indicated by an asterisk.

	Anterior unicusps															
	6	7	8	9	10									N	$\bar{X}$	δ
E. mcconnaugheyi		25	151*	15										191	7.95	0.455
E. fritzi		73*	266	32	1									372	7.90	0.531
E. sinus	62	453*	336	21										872	7.36	0.649
E. deani	3	62	604	308	11									988	8.27	0.601
E. stoutii	16	524	390*	11	1									942	7.42	0.555
	Posterior unicusps															
	6	7	8	9										N	$\bar{X}$	δ
E. mcconnaugheyi		40*	143	8										191	7.83	0.472
E. fritzi		37	270*	65										372	8.08	0.518
E. sinus	11	310*	491	60										872	7.69	0.614
E. deani		233	680	75										988	7.84	0.535
E. stoutii	4	347	570*	21										942	7.65	0.531
	Total cusps															
	34	35	36	37	38	39	40	41	42	43	44	45	46	N	$\bar{X}$	δ
E. mcconnaugheyi					4	3	11*	14	48	9	4	2		95	41.60	1.364
E. fritzi					3	5	29*	22	75	25	17	7	3	186	41.92	1.527
E. sinus	1	3	18	13	83*	46	92	39	105	16	15	1	4	436	40.10	2.089
E. deani				1	5	12	55	59	160	68	25	14	3	402	41.86	1.433
E. stoutii			3	4	84	66	126	76	93*	13	5	1	1	471	40.16	1.583

Table 6

Numbers, averages, and ranges of lengths (in mm) of first nasal barbel, left side, for 25-mm increments of total length of five species of hagfishes, genus *Eptatretus*, from the Pacific coast of North America.

	Average N(Range)				
	E. mcconnaugheyi	*E. fritzi*	*E. sinus*	*E. deani*	*E. stoutii*
200–225	3.0 3(2.6–3.5)	6.5 1(—)	2.2 6(1.5–2.6)	3.3 16(2.4–4.5)	2.3 20(2.0–3.0)
226–250	3.3 5(2.9–3.8)	5.9 4(5.6–6.2)	2.6 7(2.0–3.9)	3.5 33(2.6–4.5)	2.8 16(1.9–3.2)
251–275	3.9 8(3.1–4.6)	6.1 3(5.7–6.4)	2.8 25(2.3–3.7)	3.6 31(2.5–4.5)	3.0 52(2.0–4.0)
276–300	4.1 12(3.2–4.9)	6.9 4(6.3–7.2)	2.9 50(2.2–4.3)	4.2 30(3.3–5.3)	3.3 70(2.2–4.5)
301–325	4.2 13(3.6–5.4)	6.3 8(5.0–6.9)	3.1 71(2.0–4.4)	3.8 39(3.2–5.2)	3.5 77(2.4–4.6)
326–350	4.5 10(3.8–5.0)	6.8 24(6.5–9.6)	3.4 80(2.1–4.4)	4.1 42(2.5–5.5)	3.7 110(2.5–5.2)
351–375	4.9 11(4.1–6.3)	7.4 40(5.6–9.1)	3.1 72(2.7–5.6)	4.4 103(2.8–6.0)	3.7 127(2.5–5.1)
376–400	4.9 8(3.9–5.6)	7.8 49(6.2–8.9)	4.0 35(3.0–5.2)	4.6 202(3.0–6.6)	4.1 148(2.6–6.0)
401–425	6.1 6(5.2–7.0)	7.7 71(6.5–10.2)	4.2 17(3.5–5.4)	5.0 235(3.1–6.9)	4.2 109(2.9–5.3)

Table 6 (continued)

	Average *N*(Range)				
	E. mcconnaugheyi	*E. fritzi*	*E. sinus*	*E. deani*	*E. stoutii*
426–450	6.0 6(5.0–7.1)	8.2 50(7.4–10.2)	3.9 8(2.9–5.8)	5.1 174(3.1–7.0)	4.3 65(2.8–6.1)
451–475	6.5 2(6.5–6.5)	9.8 42(7.6–10.8)	3.8 2(3.2–4.4)	5.3 68(3.8–6.6)	5.3 33(3.7–5.9)
476–500	6.8 1(–)	8.9 21(7.2–10.3)	4.1 6(3.8–4.4)	5.4 28(4.0–6.5)	4.7 11(3.9–6.0)
501–525	6.0 2(5.8–6.1)	10.4 9(9.1–11.3)		5.2 10(4.1–5.9)	5.0 13(3.8–6.9)
526–550		10.9 7(10.3–11.7)		4.7 1(–)	4.4 8(4.3–5.4)
551–575		10.4 2(9.7–11.3)		4.6 1(–)	6.1 1(–)
576–600		10.2 2(9.5–10.8)			6.8 1(–)
N	87	273	379	1013	861

Table 7

Gill pouches, both sides, in positions relative to Areas I, II, and III of the branchial regions of five species of hagfishes (genus *Eptatretus*) from the Pacific coast of North America. Areas are identified in Figure 4. Values, left side, for type specimens are indicated by an asterisk.

Gill pouches	0	1	2	3	4	5	6	7	8	9	10	*N*	$\bar{X}$	$\acute{o}$
Area I														
E. mcconnaugheyi						2	13	23	45*	34*	9	126	7.98	1.137
E. fritzi				9	49	34*	8					100	4.41	0.763
E. sinus	2	61*	136	103	23	11	5					341	2.40	1.067
E. deani				1	46	62	11					120	4.69	0.643
E. stoutii		7	61	75*	49	19	1					212	3.07	1.023
Area II														
E. mcconnaugheyi	5	13	42*	30*	23	13						126	2.73	1.275
E. fritzi	2	7	12	43*	31	5						100	3.09	1.040
E. sinus	7	20	85	151	65*	11	1					341	2.84	0.994
E. deani	30	44	43	3								120	1.16	0.827
E. stoutii	19	38	68	65*	13	9						212	2.20	1.197
Area III														
E. mcconnaugheyi	4	25*	80	16								126	1.86	0.663
E. fritzi			9	42*	35	13	1					100	3.55	0.865
E. sinus		7	11	13	65	125*	101	17	2			341	4.97	1.229
E. deani				3	16	71	28	2				120	5.08	0.726
E. stoutii				1	3	17*	71	87	32	1		212	6.60	0.933

Table 8

Numbers and percent of occurrence of higher numbers of branchial apertures on left and right sides of five species of hagfishes (genus *Eptatretus*) from the Pacific Coast of North America.

Species	*N*	Higher on left side	Higher on right side
E. mcconnaugheyi			
Southern California	61	4 (6%)	5 (8%)
Gulf of California	37	5 (19%)	0
E. fritzi	316	81 (26%)	0
E. sinus	446	63 (14%)	7 (2%)
E. deani	1145	125 (11%)	21 (2%)
E. stoutii	1554	167 (11%)	56 (4%)
Totals	3559	445 (12.5%)	89 (2.5%)

Age and Growth of Bluefish *Pomatomus saltatrix* from the Northern Gulf of Mexico and U.S. South Atlantic Coast

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The bluefish *Pomatomus saltatrix* is a migratory coastal pelagic fish generally found in temperate and warm continental shelf waters of all oceans (Briggs 1960). The species occurs along the east coast of the United States and the coast of the Gulf of Mexico. Important commercial and recreational fisheries for bluefish exist throughout the U.S. range (Wilk 1977).

Age and growth studies have been conducted on bluefish from U.S. Atlantic waters (Hamer 1959, Backus 1962, Lassiter 1962, Richards 1976, Wilk 1977), but not from the Gulf of Mexico. The primary purposes of this study were to evaluate and use the best of several bony structures to estimate the age and determine growth of bluefish from the northern Gulf of Mexico (hereafter referred to as Gulf) and from the U.S. Atlantic coast.

Methods

Bluefish from the northern Gulf gillnet fishery were sampled monthly from 1978 through 1982 (Feb–Nov) and in the Atlantic along the southern U.S. east coast in 1980 and 1981 (Jan–July). These samples were augmented by catches from the seine and hook-and-line fisheries. The Gulf samples were collected from the coastal waters off northwest Florida and Louisiana, while Atlantic samples were taken along the coast from South Carolina to Florida.

Fork length (FL) to the nearest millimeter (mm), weight (W) to the nearest gram (g), and sex were recorded from 1190 Gulf and 842 Atlantic bluefish, and one or both otoliths (sagittae) were removed, wiped clean, and stored dry in vials. A subsample of 100 fish representing the entire size range of bluefish caught in the Gulf during May and June 1978 was selected for comparison among ageing structures. From these 100 fish, in addition to otoliths, the tenth vertebra anterior to the hypural plate was removed and scales were taken from the left side under the pectoral fin. Vertebrae were cleaned and air-dried. Both vertebrae and scales were stored dry in envelopes.

Otoliths were placed in glycerol, sulcus acousticus down, in a black dish and were examined under reflected light using a binocular-dissecting microscope with an ocular micrometer. The most legible otolith from each fish was examined for age marks. The second otolith from 25 of the bluefish was sectioned to allow interior examination. The otoliths were embedded in Lakeside 70C thermoplastic cement and, to include the locus, 2 or 3 thin sections (0.15 mm) were cut along the transverse plane, using a Buehler isomet slow-speed saw. The cement was dissolved with isopropyl alcohol, and then the otolith sections were mounted on glass slides and examined on a black background in the manner of whole otoliths.

On whole or sectioned otoliths an opaque zone (mark) preceded by a translucent (hyaline) zone (Fig. 1a) was assumed to be an age mark. Measurements (OR) were made along the longitudinal axis of the rostrum from the focus to the distal edges of the marks and of the otolith. A determination of the edge character (opaque or translucent) was made, and marks were counted. A mark was not considered complete, so not counted or measured, unless the portion of the otolith distal to it was translucent. The rostrum was selected for examination because the postrostrum had an uneven edge which proved difficult to measure.

Vertebrae were stained with crystal violet following the technique of Johnson (1979). To facilitate the observation of age marks, the vertebrae were cut in half, anterior-posteriorly, with a Dremel saw. Both halves of the vertebrae were examined under a binocular-dissecting microscope using reflected light. The most legible posterior centrum was used.

An age mark on the vertebral cone surface was counted if a prominent concentric ridge preceded by a depression was observed (Fig. 1b). Measurements were made from the vertex (focus) of the centrum to the distal edge of each mark as well as to the terminal edge of the vertebra.

Scales were cleaned in a weak solution of water and liquid detergent, then mounted between two glass slides. Scales from 15 bluefish were also impressed on plastic slides with a cold roller press. Both

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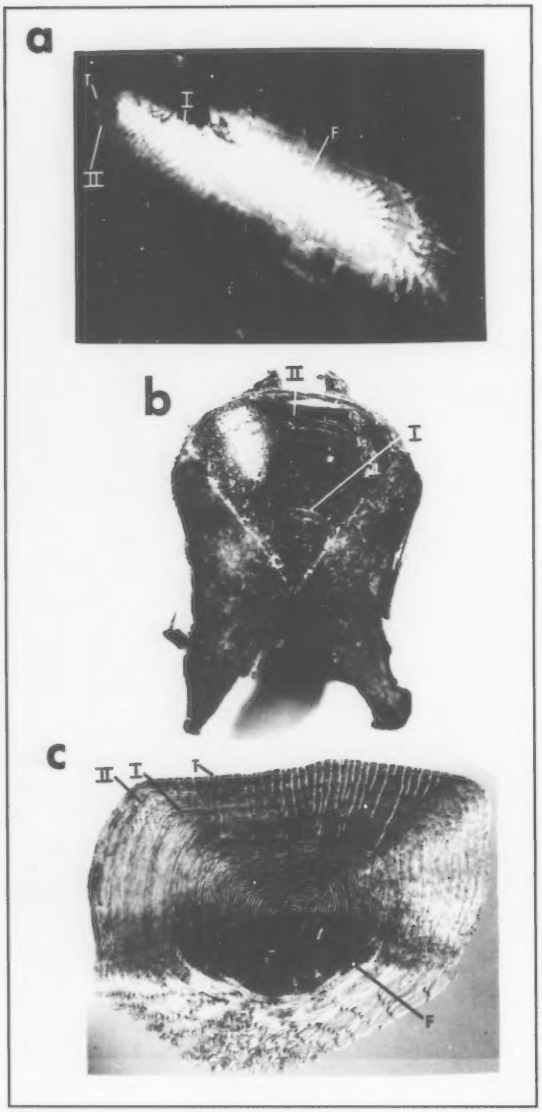

Figure 1

Otolith (a), vertebral section (b), and scale (c) from a 2+ year-old bluefish, 375 mm FL, captured in May. Distal edges of age marks are indicated by Roman numerals. F = focus; T = translucent edge.

slides and impressions were viewed on an Eberbach scale reader. The most legible unregenerated scale was examined for age marks.

On scales and scale impressions an age mark was considered to be a band of widely spaced circuli, usually with broken circuli in the anterior field and/or anastomosis (crossing over) in the lateral field, followed by a series of closely spaced circuli (Fig. 1c). Measurements were made on the projected image from the focus along a radius in the center of the anterior field to the distal edge of the marks and scale edge.

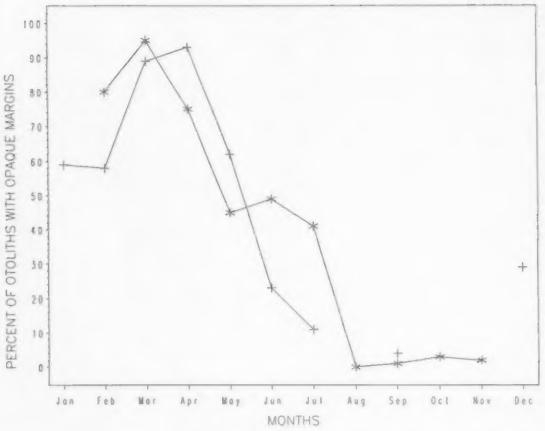

Figure 2

Percent of otoliths with opaque edges by month from Gulf of Mexico bluefish, 1978–82 (•), and U.S. South Atlantic coast, 1981–82 (+).

Two investigators each made one reading of a set of otoliths, vertebrae, and scales from 100 bluefish. All examinations were made without reference to fish length or interpretations of the other investigator.

Computer analyses and plots were accomplished using SAS (Ver. 6.03) software. Backcalculations of length-at-age were accomplished with a program written by the author using means weighted by multiplication of number of samples. Gulf and Atlantic bluefish were analyzed separately. Separate analyses by sex included regressions of fork length and natural log of fork length on otolith length. Least-squares regressions were used to backcalculate length-at-age for males and females separately (Ricker 1975). Multiple regression of sex and age was run to determine difference in length-at-age by sex. Von Bertalanffy theoretical growth curves were calculated using weighted-mean backcalculated fork lengths. The growth equation (von Bertalanffy 1938, 1957) was the following:

$$l_t = l_\infty (1 - e^{-k(t-t_0)})$$

where l_t = length at age,
l_∞ = asymptotic length,
k = growth coefficient, and
t_0 = time when length would theoretically be zero.

Table 1
Backcalculated weighted mean fork lengths of bluefish.

Estimated age group	Number	Mean length at capture (mm)	Mean backcalculated length-at-age (mm)							
			1	2	3	4	5	6	7	8
From northern Gulf of Mexico, 1978–82										
1	389	364	322							
2	69	441	284	400						
3	30	640	307	415	488					
4	27	719	285	430	515	575				
5	50	745	272	411	510	572	622			
6	29	766	283	424	517	579	628	673		
7	11	766	295	423	512	576	627	668	708	
8	6	767	275	423	530	598	650	695	728	766
Weighted mean			308	413	509	576	627	675	715	766
Annual increment				105	96	67	51	48	40	51
Number			611	222	153	123	96	46	17	6
From U.S. Atlantic coast, 1980–81										
1	389	382	299							
2	161	394	275	362						
3	26	446	265	350	412					
4	12	536	261	342	421	473				
Weighted mean			290	361	415	473				
Annual increment				69	56	58				
Number			588	199	38	12				

Results and discussion

Agreement between investigators in enumeration of marks was highest (92%) with whole otoliths. Lower agreements were attained for scale impressions (67%), vertebrae (33%), and scales (24%). In comparison of whole otoliths with cross-sections taken from the other otolith of a pair, investigators agreed 70% of the time. The close spacing of marks in the sections caused more disagreement in mark enumeration than did the wider spacing in the rostrum of the whole otolith. Also, fractures sometimes occurred in preparation of thin sections, making enumeration of marks on cross-sections of otoliths a less viable option. In addition, 30 otoliths were examined and no difference was found in mark counts on either the rostrum or postrostrum of the otolith or between pairs of otoliths.

To use otoliths, or any structure, for age determination, the deposition of regular detectable age marks is essential. Because samples were obtained from catches of the fishery, no accepted method of direct validation could be employed. However, indirect evidence was established by correlation of the observed mark formation at the distal edge of the rostrum with month. Despite the lack of samples for all months, the results suggested that opaque marks were formed annually in late winter or early spring around March and April in the Gulf and Atlantic samples, respectively (Fig. 2). Gulf bluefish show an unexpected flattening of the curve in June and July. The reason is not known, but a likely hypothesis is a stress-induced check from environmental causes. An alternate hypothesis could be a multiple spawning. However, there are no reports of a summer spawn of bluefish in the Gulf. Backcalculation of length at the time of mark formation is dependent on the relationship between the size of the ageing structure and fish length. Improved fit of the otolith radii (OR) to length relationship occurred when natural log transformation was used for fork length. The equation for Gulf bluefish was $LOG(FL) = 4.200 + 0.389 \times OR$ ($r^2 = 0.86$). The equation for Atlantic bluefish was $LOG(FL) = 4.822 + 0.248 \times OR$ ($r^2 = 0.61$).

Sexes were pooled for analysis because no significant difference ($\alpha > 0.10$) was found between mean backcalculated fork lengths of sex at age. Studies of Hamer (1959) in the New York Bight, Lassiter (1962) off North Carolina, and Richards (1976) off Long Island also showed no appreciable difference in growth between sexes. The length-weight equation for Gulf bluefish was $W = -10.02 \times FL^{2.80}$ and was $W = -9.18 \times FL^{2.77}$ for Atlantic bluefish.

Backcalculated lengths-at-age from Gulf and Atlantic bluefish were similar to the respective lengths at

capture (Table 1). The differences were attributed to growth after mark formation. Gulf bluefish were consistently greater in length for age compared with Atlantic bluefish. The difference gradually increased through age-4, the maximum age of the available Atlantic samples.

The Gulf samples included large fish (>600 mm FL) in relatively large numbers (>30% of the sample) only in May and June 1978. During other years, the large fish made up only 4% or less of the Gulf samples. Bluefish of this size are not commonly found in the Gulf. Fable et al. (1981) reported that these fish were decidedly larger than Gulf bluefish observed in 1973 and 1977. Atlantic samples included fish estimated to be no older than age 4 and FL less than 600 mm.

A general comparison with some previous bluefish studies was made (Fig. 3). All other studies used scales to age bluefish and did not report validation. Scale studies were used, as no similar otolith studies could be obtained. Wilk (1977) analyzed scales from bluefish sampled along the Atlantic coast. His results showed slower growth to age-1 than either Gulf or Atlantic samples from this study. By age-2 a larger rate of growth had converged his reported lengths to just short of the Gulf samples from this study, a relationship maintained until age-7 at which point small sample sizes may have contributed to errors. Reported lengths-at-age from scales of Long Island Sound bluefish (Richards 1976) were similar to those of this study. North Carolina spring-spawned bluefish aged by scales (Lassiter 1962) fall within range of Gulf bluefish from this study, but have shorter lengths at each age.

The von Bertalanffy (1938, 1957) theoretical growth parameters derived from this study are:

$$\text{Gulf: } k = 0.180,\ l_\infty = 944,\ t_0 = -1.033$$
$$\text{Atlantic: } k = 0.096,\ l_\infty = 1{,}019,\ t_0 = -2.493.$$

Growth coefficient (k) for Gulf bluefish is within the range of those reported by Lassiter (1962) for North Carolina spring-spawned (0.103) and summer-spawned (0.342) and by Manooch (1979) for Gulf and Atlantic maximum age-8 (0.230) and maximum age-9 (0.340) bluefish. The high growth coefficient of Gulf bluefish reflects the relatively rapid initial growth. The large bluefish taken in the summer of 1978 may influence this coefficient.

Otoliths appear to be better than either scales or vertebrae for ageing Gulf bluefish. Based on the percent of opaque edge occurrence and the close fit with other studies, it appears that age marks on the otoliths of Gulf bluefish are formed annually. Direct validation of age, which was not possible in this study, should be included in future studies. The cause of a higher percent of otoliths with opaque edges in the months of June and July in Gulf bluefish should also be a point of further investigation.

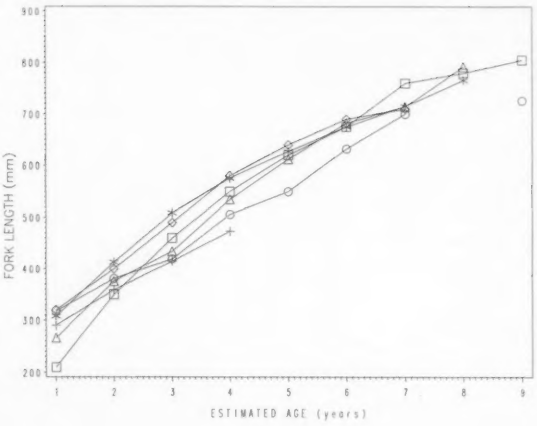

Figure 3

Mean length of bluefish from the Gulf of Mexico and the U.S. Atlantic coast by age in years from this and other published studies. Northern Gulf of Mexico, this study (•); U.S. South Atlantic coast, this study (+); Long Island Sound, NY (Richards 1976), (◇); New York Bight (Hamer 1959), (○); Atlantic coast (Wilk 1977), (□); North Carolina (Lassiter 1962), (△).

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Food Habits of Larval Sablefish *Anoplopoma fimbria* from the Bering Sea

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Sablefish *Anoplopoma fimbria* spawn at depths exceeding 400 m (Mason et al. 1983) and their larvae ascend to surface waters soon after hatching (Kendall and Matarese 1987). While in the neuston, they are subjected to highly variable oceanographic conditions. A comparison of the diet of sablefish larvae collected off Oregon and Washington between years that differed markedly in oceanographic conditions (1980 and 1983) revealed a difference in the size of copepods that were ingested (Grover and Olla 1987). Clearly diet can vary between years in one location in response to oceanographic conditions, yet it is unclear how larval diet might vary between distant geographical areas of differing oceanographic conditions.

The aim of the present work was to examine the food habits of larval sablefish that were collected in the Bering Sea in 1979 and compare these findings with those from an earlier study of specimens collected off Oregon and Washington (Grover and Olla 1986, 1987).

Methods

Sablefish larvae were collected during 1979 as part of an ichthyoplankton survey in the Eastern Bering Sea (Walline 1981). Samples were collected using a modified Sameoto neuston sampler, 0.3 × 0.5 m with 0.505-mm mesh, towed at the surface for 10 minutes at 2–3 knots. Surfacewater temperatures ranged from about 6°C to just over 8°C. Collections were made from the RV *Miller Freeman* between 17 June and 10 July 1979.

All specimens ($N = 127$) from 5 stations (Fig. 1) where larval densities were at least 1/10 m^2 surface area were examined. This represents more than 40% of the total number of sablefish larvae that were collected in 1979.

Larvae were preserved in 10% formalin and were switched into 5% formalin after sorting. Standard length (SL) of each larva was measured, the digestive tract was removed, and contents from the entire digestive tract were identified.

Diet was analyzed in terms of numerical percentage composition (%*N*), percent frequency of occurrence (%FO), and volumetric percentage composition (%VOL). Prey volumes were calculated from prey dimensions (Grover and Olla 1987). An index of relative importance (IRI = (%*N* + %VOL) × %FO) (Pinkas et al. 1971) was used for a more comprehensive assessment of prey importance. Data were examined by larval size group (12–15 and 16–23 mm SL).

Prey was categorized as diatoms, copepod eggs, copepod nauplii, *Oithona similis*, *Pseudocalanus* sp. adults and copepodites, *Acartia longiremis*, *Acartia* spp., unidentified copepods, amphipods, and all other prey items.

Prey widths that were used to examine prey-size selection were obtained only from items that were not badly broken or flattened. Over 2900 prey items were measured.

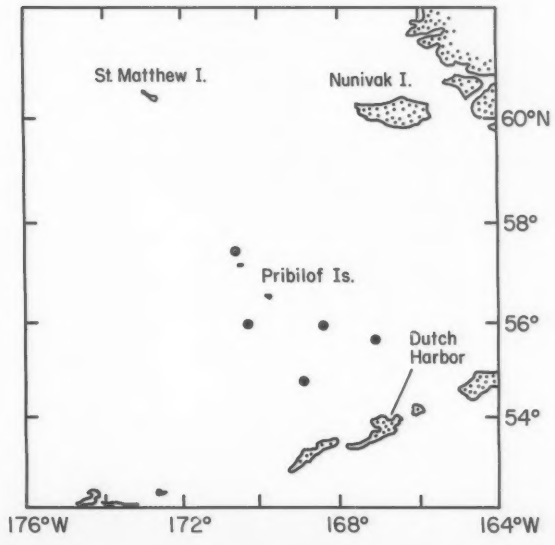

Figure 1
Location of collection stations in the eastern Bering Sea.

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Median widths of diatoms were the smallest (0.01–0.10 mm), followed by copepod eggs, nauplii, and *O. similis* (0.11–0.20 mm), *Pseudocalanus* copepodites, *A. longiremis*, *Acartia* spp., unidentified copepods, and other prey (0.21–0.30 mm), and *Pseudocalanus* sp. adults and amphipods (0.31–0.40 mm).

Results

A single prey-size class was most often ingested by all larvae (Fig. 2A). While both large and small larvae consumed small prey, the ingestion of larger prey by large larvae resulted in the two curves being significantly different ($P<0.01$, Kolmogorov-Smirnov test; Conover 1980). The shared mode of the two curves was attributed to large larvae ingesting a number of small prey items, particularly copepod eggs (0.11–0.20 mm) (Table 1). When we eliminated copepod eggs from the analyses, assuming that they were taken incidentally in the course of ingesting adult female *Pseudocalanus* sp., the prey-size distribution of small larvae did not change noticeably (Fig. 2B). But the removal of copepod eggs from the diet of large larvae shifted the prey-size mode towards larger prey.

Copepod nauplii were the primary prey of small larvae (Table 1). *Pseudocalanus* sp. also comprised a major portion of the diet, with adults and copepodites nearly equal in importance. Unidentified copepods made a small contribution, while *Acartia* spp., *Oithona similis*, and copepod eggs were rather insignificant in the diet of small larvae.

Copepods were the primary prey of large larvae (Table 1), with *Pseudocalanus* sp. adults predominant over copepodites and all other species. A large number of copepod eggs were ingested, while amphipods, unidentified copepods, *Acartia longiremis*, and copepod nauplii made progressively smaller contributions to the diet. The relatively large size of amphipods likely contributed to their being ingested only by large larvae.

The mean number of prey items ingested by small larvae was 26.9, compared with 34.1 by large larvae. The incidence of feeding was 100%.

Discussion

The pattern of prey-size selection observed in the Bering Sea contrasts with the pattern seen for larvae collected off the Oregon and Washington coasts in 1980 (Grover and Olla 1986). In each study functional breaks in diet (e.g., the shift away from dependence on copepod nauplii) were used to define larval size groups. The Oregon–Washington collections were categorized into three size groups: 8.2–12.5, 12.6–20.5, and 20.6–28.5 mm SL. Each size group favored a different peak prey size, with the smallest larvae ingesting the smallest prey, and the largest larvae ingesting the largest prey (Grover and Olla 1986). However, peak prey sizes for the two size groups from the Bering Sea were the same as long as copepod eggs were included in the analyses. Their removal shifted the prey-size utilization curve of large larvae in the Bering Sea towards larger prey.

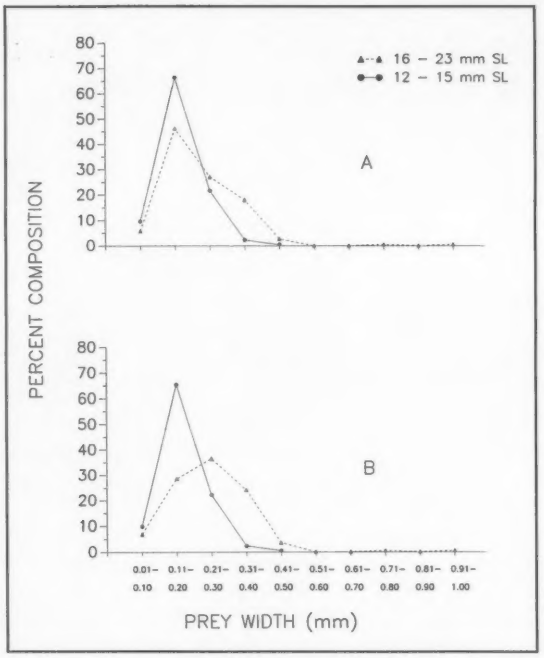

Figure 2
Size of prey selected by two size classes of larval sablefish (12–15 and 16–23 mm SL) in the Bering Sea in 1979: (A) including copepod eggs, (B) omitting copepod eggs.

Copepod eggs had a greater impact on the diet in the Bering Sea than off Oregon due to a difference in the biology of the dominant copepod species ingested in the two regions. The dominant copepod in the diet of large larvae collected off Oregon in 1980 was *Paracalanus parvus* (Grover and Olla 1987), a species that broadcasts its eggs into the sea (Checkley 1980). *Pseudocalanus* sp., the dominant copepod in the diet of larvae collected from the Bering Sea, carries its eggs (Corkett and McLaren 1978) which could thus be ingested incidental to the adults. Nevertheless, as female copepods with eggs were not observed in sablefish guts, and as other copepods that broadcast their eggs (such as all *Acartia* spp.) contributed to the diet, it remains a possibility that some eggs were ingested independently

Table 1

Composition of the diet of larval sablefish in the Bering Sea in terms of the Index of Relative Importance (IRI) and its components: Numerical percent composition (%*N*), frequency of occurrence (%FO), and volumetric percent composition (%VOL), by size class.

	Larval size class							
	12–15 mm				16–23 mm			
Prey	%*N*	%VOL	%FO	%IRI	%*N*	%VOL	%FO	%IRI
Diatoms	0.2	<0.1	4.5	<0.1	3.3	<0.1	30.8	0.8
Copepod eggs	2.6	0.3	22.7	0.4	20.2	0.8	74.4	11.2
Copepod nauplii	74.1	41.6	100.0	77.9	12.9	3.0	43.6	5.0
Oithona similis	2.4	2.5	27.3	0.9	5.0	2.2	38.5	2.0
Pseudocalanus sp. adults	4.2	23.6	39.8	7.4	23.7	55.7	92.3	52.7
Pseudocalanus copepodites	9.6	17.8	50.0	9.2	9.4	8.2	74.4	9.4
Acartia longiremis	0.3	0.8	1.1	<0.1	8.4	8.6	41.0	5.0
Acartia sp.	2.4	4.7	19.3	0.9	2.1	1.7	38.5	1.1
Unident. copepods	3.7	7.4	40.9	3.1	7.5	6.3	56.4	5.6
Amphipods					7.2	13.2	48.7	7.1
Other	0.5	1.2	10.2	0.1	0.3	0.3	7.7	<0.1

of females. However, since the number of copepod eggs in the diet appeared to be positively correlated with the number of adult *Pseudocalanus* sp. ingested, we conclude that most copepod eggs were probably attached to adult female *Pseudocalanus* sp. when they were ingested. The mechanical action of ingestion most likely liberated the eggs from their delicate egg sacs (see Grover 1990). These data suggest that copepod eggs may be important in the diets of larval sablefish and other species in the Bering Sea.

In contrast to the larval diet off Oregon and Washington, copepods >2 mm were inconsequential in the diet of larvae in the Bering Sea. While copepod species with southern affinities were absent from the diet of sablefish larvae collected in the Bering Sea, species with northern affinities, i.e., *Pseudocalanus* sp. and *A. longiremis*, occurred more frequently in the diet of larvae collected in the Bering Sea than off Oregon (Grover and Olla 1987). Euphausiid larvae, appendicularians, and pteropods were absent from the diet of sablefish larvae collected in the Bering Sea, while they made a noticeable contribution to the diet of sablefish larvae collected off Oregon.

Specific differences in prey items could be expected when comparing geographically separated populations; however underlying principles of prey-size selection are assumed to be universal in nature (Hunter 1981). We looked beyond the initial data plots and found a biological explanation as to why the size of prey consumed by large larvae in the Bering Sea differed from the pattern observed off Oregon (Grover and Olla 1986). Our data revealed that copepod eggs have such a confounding influence on prey-size distributions that the mode of their ingestion (i.e., free-floating vs. attached to adults) must be recognized in order to adequately interpret prey-size selection patterns.

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We wish to thank C.B. Miller for sharing his knowledge of copepod biology, and Art Kendall for his continued interest in the early life history of this species.

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Movement of Tagged Lingcod *Ophiodon elongatus* at Neah Bay, Washington

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Lingcod *Ophiodon elongatus* is an important component of Washington's coastal commercial and sport fisheries (Jagielo 1989). Female lingcod comprise most of the offshore commercial landings, grow faster than males, and attain a larger size. Males predominate in the nearshore sport catch, are typically smaller than females, and perform a nest guarding role during reproduction. These characteristics of the coastal lingcod population suggest the need for an integrated stock assessment which addresses males and females separately and takes the geographic distribution and migratory behavior into account.

This paper reports the movement of lingcod tagged nearshore in the western Strait of Juan de Fuca near Neah Bay, Washington, during 1986–89. Results are presented for tags recovered through 1989 and analyzed by sex and size for extent and direction of movement. I also evaluated tag retention of a wire spaghetti tag applied on the preopercular plate as an alternative to strap, anchor, or dart tags used previously for lingcod tagging (Chatwin 1958, Forrester 1973, Cass et al. 1983, Mathews and LaRiviere 1987).

Methods

From 1986 to 1989, 3478 lingcod were tagged using a chartered commercial vessel trolling with 6–10 jigs from a hydraulic gurdy. Each year fishing occurred from mid-March to mid-April in advance of the sportfishery opening on 15 April. Only fish not injured by capture were tagged and released. All tagged fish were measured to the nearest millimeter, and sex was determined by noting the presence of anal papillae in males.

The tagging area was within 3 miles of the shoreline in the vicinity of Neah Bay, Washington, and extended from the Sekiu River to Makah Bay (Fig. 1). In 1986, the tagging effort was distributed evenly among areas NB-1, NB-2, and NB-3. Area NB-4 was added in 1987, and effort was distributed evenly among the four areas from 1987 to 1989. Most of the tagging occurred at depths between 15–25 m.

In 1986 two tag types were released: 481 fish were tagged with a large dart tag (Floy FT-1) applied dorsally, and 487 fish were tagged with a wire spaghetti tag (Floy FT-4) twist-tied to the preopercular plate. Fish were alternately tagged with one of the two tag types and were released back into the population. Recaptures from 1986 to 1989 for the two tag types are shown in Table 1. In 1987 and 1988, 207 fish were double-tagged with the spaghetti tag to evaluate tag shedding. Through September of 1989, 20 of the double-tagged fish were recovered, all with both tags in place. Since tag shedding appeared to be negligible for the spaghetti tag, only fish released with the spaghetti tag (2997 lingcod) were analyzed for movement trends in this paper.

Recapture information, including the date and location of capture, was obtained both by direct interviews with fishermen and by voluntary returns submitted by fishermen. A $10 reward was paid for the return of tags, which was available directly on landing at Neah Bay.

Migratory and nonmigratory lingcod were defined as fish recaptured at distances greater than or less than 8.1 km (5 miles) from the tagging location, respectively. This reference distance was selected to enable comparisons with previous tagging studies. Chi-square contingency-table analysis was used for comparing release length-frequency distributions of migratory and nonmigratory recoveries and migrational tendency by sex. A chi-square goodness-of-fit test was used to test the null hypothesis that the release length distribution of recaptured lingcod was the same as the release length distribution of all tagged lingcod. Length-frequency distributions were grouped into 5-cm intervals and pooled at the tails so that no expected cell frequency was <1.0 and no more than 20% of the expected cell frequencies was <5.0 (Zar 1974, p. 50). One-way analysis of variance was used to test the null hypothesis that the mean time at liberty was the same for fish that had migrated different distances.

Results

Through September 1989, 393 (13.1%) tagged lingcod were recaptured (Table 2). The percent recaptured for each release group ranged from 9.96% in 1989 to 18.89% in 1986. The lower recovery rate for the 1989 release is probably a reflection of fewer recovery years as compared with releases from 1986 to 1988.

The length distribution of tagged lingcod by sex are shown in Figure 2a. Of all tagged lingcod, 99% were sexed; 84% of this sample were

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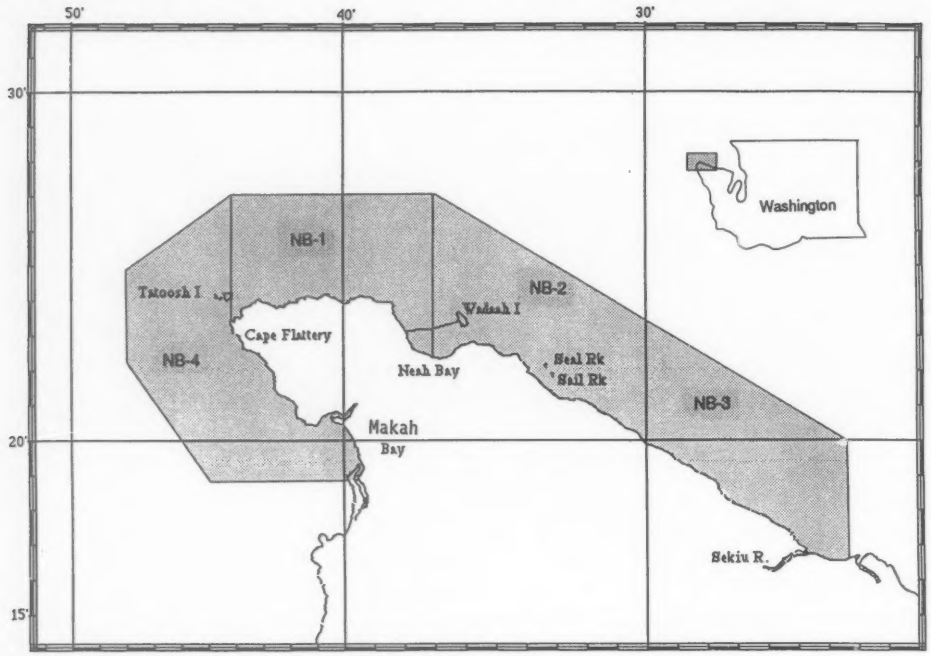

Figure 1
Lingcod tagging area at Neah Bay, Washington.

Table 1
Rates of recapture of tagged lingcod for two types of tags released in 1986.

Tag type	No. tagged	No. tags returned by fishermen 1986	1987	1988	1989	Total	% returned
Large dart (Floy FT-1)	481	41	25	7	1	74	15.38
Spaghetti (Floy FT-4)	487	47	29	13	3	92	18.89

Table 2
Number of lingcod tagged, 1986–89, and recaptured through 1989 by year of recapture.

Year tagged	No. tagged	1986	1987	1988	1989	Total	% recaptured
1986	487	47	29	13	3	92	18.89
1987	564	0	36	20	15	71	12.59
1988	982	0	0	79	55	134	13.64
1989	964	0	0	0	96	96	9.96
Total	2997	47	65	112	169	393	13.11

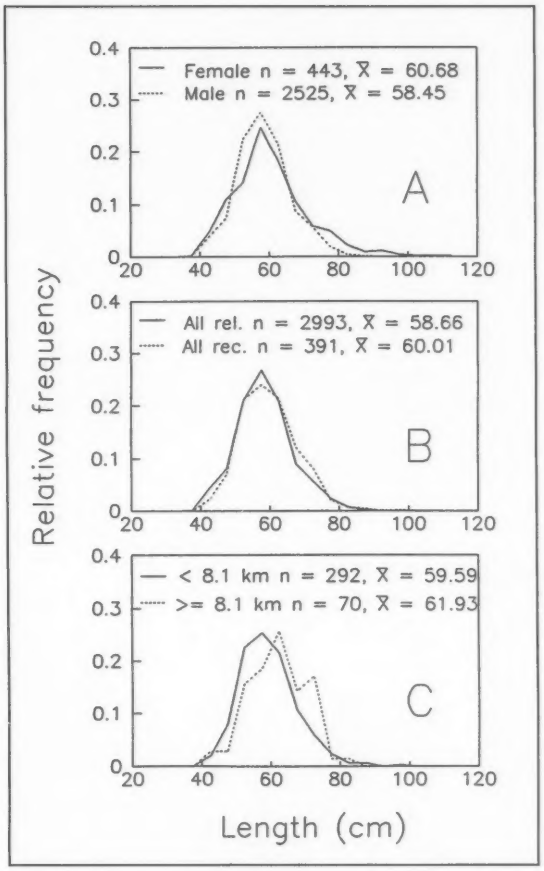

Figure 2

Length-frequency distributions of tagged lingcod. (A) Known male and female lingcod tagged; (B) release length distribution of all lingcod released and all lingcod recovered; (C) release length distribution of all lingcod recovered <8.1 km from release location and all lingcod recovered ≥8.1 km from release location.

males. The average size of tagged males (58.45 cm) was less than the average size of females (60.68 cm). Based on the length-at-maturity values of 46 cm for males and 76 cm for females (Mathews and LaRiviere 1987), approximately 95% of the tagged males were mature, and approximately 10% of the tagged females were mature at the time of tagging.

The average size of all tagged fish recaptured (60.01 cm) was greater than the average size of all tagged fish released (58.66 cm) (Fig. 2b). The null hypothesis that the length distribution of all recaptured lingcod is the same as that of all tagged lingcod was rejected (χ^2 = 14.91 with 7 df; P = 0.0371).

The average size of fish considered migratory (61.93 cm) was greater than those considered nonmigratory (59.59 cm) (Fig. 2c). The null hypothesis that migratory fish had the same length distribution as nonmigratory fish was rejected (χ^2 = 51.42 with 5 df; P<0.00001).

Of the 363 lingcod with known tagging and recapture locations, 70 (19.3%) were recaptured >8.1 km (5 miles) from the tagging location and were considered migratory, while the remaining 293 were recaptured within 8.1 km of the tagging location and were considered nonmigratory (Table 3). Of those that migrated, 46 were recaptured from 8.1 to 50 km from the tagging site, and 24 were recaptured >50 km from the tagging site.

Relative to the tagging location, most of the migratory recaptures were westward and out of the Strait of Juan de Fuca as opposed to eastward and inside the Strait. Of the 70 lingcod judged to be migratory, 54 were recaptured west and north/south of the tagging location, while only 16 were recaptured east and north/south of the tagging location (Table 3). The null hypothesis that male and female tagged lingcod were as likely to be recaptured east and north/south as opposed to west and north/south) of the tagging location was rejected (χ^2 = 20.62 with 1 df; P<0.00001). Recaptures came from as far north as Queen Charlotte Sound (241 miles), as far south as Cape Falcon (149 miles), and as far east in the Strait of Juan de Fuca as Crescent Bay (36 miles). Most of the migratory fish (25) were recovered on trawl grounds off the Washington coast and included those in the vicinity of Cape Flattery (5), the Cape Flattery Spit (9), Umitilla/La Push (4), Destruction Island (4), and Cape Elizabeth (3).

Table 3

Distribution of recoveries of tagged lingcod by distance and direction of migration.

		8.1–50 km			>50 km			Recaptured	
No. tagged	<8.1 km	East	West	Total	East	West	Total	No.	%
2997	293	15	31	46	1	23	24	393*	13.11

*Includes 30 recaptures with unknown recapture location.

Table 4
Distribution of recaptured lingcod by sex and distance of migration.

Sex	Total released	Number recaptured				Recaptured	
		<8.1 km	8.1–50 km	>50 km	Unknown distance	Total	%
Male	2526	245	42	24	23	334	13.22
Female	443	47	4	0	6	57	12.87
Unknown	28	1	0	0	1		
Total	2997	293	46	24	30	393	13.11

Thirteen were recovered on Canadian trawl grounds including La Perouse Bank (8) and Swiftsure Bank (4). Twenty of the migratory recaptures occurred within the tagging area between Makah Bay and the Sekiu River (Fig. 1), and 12 recaptures were made east of the study area in the Strait of Juan de Fuca.

Of fish with known sex and recapture location, a higher proportion of male lingcod were migratory as compared with female lingcod. Of 311 male recaptures, 66 (21.2 %) were judged to be migratory, while 4 of 51 female recaptures (7.8%) were considered migratory (Table 4). The null hypothesis that male and female recaptures were equally likely to be migratory was rejected ($\chi^2 = 4.20$ with 1 df; $P = 0.0402$ with Yates correction).

The time span between tagging and recapture for all recaptured lingcod averaged 237.6 days and ranged from 6 to 1197 days (Table 5). The null hypothesis that the average time span between tagging and recapture was the same for fish recaptured at different distances was not rejected ($F_{2360} = 1.50$; $P = 0.2240$).

Table 5
Time span between date of tagging and date of recapture of tagged lingcod with known date of recapture.

Distance between release and recapture	No. recaptured	Time span (days)	
		Mean	Range
<8.1 km	293	224.91	18–1197
8.1–50 km	46	251.85	36–1122
>50 km	24	306.63	78–770
Total	393*	237.61	6–1197

*Includes 30 fish with unknown distance traveled.

Discussion

This study gives qualitative evidence that a portion of the nearshore lingcod population in the vicinity of Neah Bay is vulnerable to the offshore trawl fishery; however, fishery tag recapture data, unadjusted for differential fishing effort, are inadequate to make quantitative statements about the net mixing rates of fish between areas. Clearly, from a harvest management perspective, it is important to know whether offshore stocks of lingcod contribute to nearshore recruitment, or vice versa, since valued fisheries operate in both areas.

Previous studies in the Strait of Juan de Fuca and Strait of Georgia have reported variable lingcod movement and indicate some exchange between inside and outside waters. Hart (1943) observed that fish tagged in the vicinity of the Strait of Juan de Fuca and Seymour Narrows made more extensive migrations than fish tagged in other adjacent inside waters. Of 1993 fish released during 1939–43, 209 were recovered of which 34 (16%) traveled distances >8.1 km (5 miles). For 342 recoveries from tags released in the Strait of Georgia during 1943–54, 73 (21.3%) were recaptured within 1.6 km (1 mile) and 32 (9.3%) were recaptured >8.1 km from the point of release. Of those recaptured >8.1 km, the average time at liberty was 3 years and the net movement was northwesterly within the Strait (Chatwin 1956). Mathews and LaRiviere (1987) reported that of 1692 lingcod tagged during 1976–81 in the eastern Strait of Juan de Fuca and in the vicinity of the San Juan Islands, 74 (49.6%) of 149 fish recovered moved >8.1 km and were judged to be migratory. Most recaptures were south or west of the tagging site; the predominant pattern of movement was south and west through the Strait of Juan de Fuca. Fish tagged in the eastern Strait of Juan de Fuca migrated more than fish tagged in the San Juan Islands. Five recaptures were reported from the Pacific Ocean. The longest movement to the northeast was to Porlier Pass, British Columbia; the longest movement to the southwest was off Newport, Oregon.

Previous offshore tagging studies have reported some movement between the various offshore fishing banks. Reeves (1966) reported that of 437 tagged on La Perouse (Forty Mile) Bank in June of 1960, 284

were recovered of which 74% were captured in the area of release, 21% had uncertain recovery location, and 5% were recaptured away from Forty Mile Bank (as far as Cape Flattery to the south and Ucluelet-Barkley Sound to the north.) The majority of all recaptures (82%) occurred within a 6-week period following the release because of an intensive trawl fishery for lingcod in the vicinity of tagging on Forty Mile Bank. Forrester (1973) reported the release of 2000 tagged lingcod on the Lennard Island trawling grounds in September of 1964; 535 were recovered with known locations of which 92 (17.2%) moved from the tagging site. Most of the fish recovered away from the tagging site were recaptured on Big Bank (southern La Perouse Bank) to the south. Fish were recaptured from as far as Cape Russell to the north and as far as Cape Flattery to the south. Most recaptures occurred in the summer months of the year following tagging (A.J. Cass, Pac. Biol. Stn., Dep. Fish. Oceans, Nanaimo, BC, Canada, pers. commun.). Jack Robinson (Oreg. Dep. Fish. Wildl., Newport, OR, pers. commun.) reported the tagging of 3800 lingcod in offshore waters near Newport, Oregon in July of 1978. Within 17 months, approximately 10% of the tagged fish were recovered of which approximately 9% were recovered away from the area of tagging. Mathews and LaRiviere (1987) reported the results of H. Horton from 522 lingcod tagged off Depot Bay on the central Oregon coast during June 1978–January 1982. Of 19 recaptures reported through 1985, 10 had not moved significantly and 9 (47%) had migrated more than 10 km. Of those that migrated, 2 went a distance of more than 100 km.

Chatwin (1956) reported evidence of homing behavior in Strait of Georgia lingcod. Of 14 lingcod captured at Entrance Island and transported 9.7 km (6 miles) to Departure Bay (Hart 1943), 4 were subsequently recaptured at Entrance Island, and one at Newcastle Island (between Entrance Island and Departure Bay) within 2 years of release. Buckley et al. (1984) reported evidence of homing behavior in Strait of Juan de Fuca lingcod. Of 187 adult lingcod transferred from the eastern Strait of Juan de Fuca to Pulali Point in Hood Canal in 1978, 9 recoveries all were recaptured at distances >8.1 km from the release site. Of the 9, 7 were recaptured northward in the direction of their original capture site.

My results at Neah Bay show more lingcod migratory behavior than most of the previous studies, but less than that reported in the eastern Strait of Juan de Fuca (Mathews and LaRiviere 1987). I found 70 of 363 recaptures (19%) to be migratory. Of the 70 that migrated, 24 (34%) moved in excess of 50 km. Mathews and LaRiviere (1987) reported 74 of 149 recaptures (50%) to be migratory, of which 13 (18%) moved over 50 km. The difference in percent migratory could be due to differences in exploitation rates. The Neah Bay tagging was conducted in March and April, and most tags were recaptured in the spring and summer months immediately following tagging. Most of the tags came from the intense sportfishery operating in the vicinity of Neah Bay, which may have removed potential migrants. Most of those that moved over 50 km escaped the sportfisheries and were recaptured on trawl grounds offshore. In the eastern Strait of Juan de Fuca, tagging was conducted through May and most of the recaptures occurred the year following tagging by Canadian trawlers on Constance Bank (Mathews and LaRiviere 1987). These fish were probably not subject to the same recreational fishing pressure in the vicinity of tagging, and have had a greater opportunity to migrate. The difference in the relative proportion of fish moving >50 km could be due to the distances from release sites to trawling sites; Constance bank is 18 km west of Middle Bank, where much of the eastern Juan de Fuca tagging occurred, while most of the coastal trawling occurs over 50 km from the Neah Bay study area.

The predominance of male fish tagged at Neah Bay can be explained by the different bathymetric distribution of the two sexes. Others have reported that lingcod are distributed by depth according to sex and size; larger fish (mainly females) inhabit deep banks or reefs, while smaller fish (typically males) inhabit the shallower reefs nearshore (Chatwin 1956, Forrester 1973, Miller and Geibel 1973, Cass et al. 1984). Mathews and LaRiviere (1987) noted a similarly skewed sex ratio for fish tagged nearshore in the eastern Strait of Juan de Fuca.

While the results of this and previous nearshore tagging studies give evidence of nearshore to offshore movement, a coherent pattern is not evident and a reliable working model of coastal lingcod migration is not yet available. Migratory recaptures from the present study were typically larger at the time of release than nonmigratory fish, suggesting a size threshold for movement; however, Mathews and LaRiviere (1987) failed to show a relationship between size at release and migratory tendency, and Hart (1943) concluded that large lingcod move less than small lingcod and that "some but not more than 5% of lingcod are more or less migratory during each year." Since the tagging at Neah Bay occurred nearshore in a narrow depth range (15–25 m) where the relative abundance of females is low, the effect of sex and size on lingcod movement reported here is likely biased with reference to the population as a whole. This depth-related bias may explain the discrepancies between this and other studies with regard to lingcod movement.

Some level of female movement from offshore to nearshore areas for spawning is implied by the high

relative abundance of females at depth, though the nature and extent of such spawning migrations is poorly understood. It is unclear, for instance, whether females spawning nearshore reside nearby at depth and make vertical seasonal migrations to spawn, or whether female lingcod migrate seasonally from the deep offshore trawling grounds to spawn nearshore. Such movements have been widely accepted as fact, though tagging experiments to date have failed to confirm a seasonal mass spawning migration (Miller and Geibel 1973).

An appropriate tagging study design to model coastal lingcod movement will require tagging in both nearshore and offshore areas and the estimation of both the probability of survival as well as the probability of capture across the time-area strata. To separate movement from survival, a minimum of three samples is needed. Iwao (1963) and Arnason (1972) gave models under this scenario, but only for the case with multiple recaptures. These approaches are not applicable to most fisheries tagging studies in which individuals are recaptured once by a commercial or recreational fishery and recovered dead. Potentially more applicable to fisheries tagging studies, Schwarz (1988) and Schwarz and Arnason (1990) have extended the traditional exploitation-based models of Brownie et al. (1985) to include tag recoveries over both time and space, and Hilborn (1990) recently provided a general framework for analysis of movement and mortality which incorporates a population dynamics and movement model using a maximum-likelihood minimization approach.

In conclusion, this study gives evidence that a component of the lingcod population at Neah Bay is exposed to fishing mortality from the offshore trawling fleet. Research is needed to yield quantitative estimates of lingcod mixing rates, stratified by sex and size, between the nearshore and offshore fishing grounds. These mixing rates will be essential to establish mortality rates by sex and age for the population as a whole, to clarify the collective impact of the nearshore and offshore fisheries on the coastal lingcod population.

Acknowledgments

This research was supported by the Washington Department of Fisheries and the Federal Aid in Sport Fish Restoration (Wallop-Breaux) Program. Special thanks are due to Donald "Bud" Carleson, skipper of the commercial troller *Paul Revere*, for his knowledge of lingcod habits and help in capturing lingcod for tagging.

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Captive Tunas in a Tropical Marine Research Laboratory: Growth of Late-larval and Early-juvenile Black Skipjack *Euthynnus lineatus*

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Little is known about the biology of tunas during larval and early-juvenile stages because they are relatively inaccessible to scientists. In the eastern Pacific Ocean fishermen seldom catch juveniles of less than about 30 cm in length. Concurrent laboratory and field studies of tuna growth and mortality are important to gain insight into the recruitment process. These considerations motivated the Inter-American Tropical Tuna Commission (IATTC) to establish a research center at Achotines Bay in the Republic of Panama, a site located near tuna spawning grounds (Fig. 1).

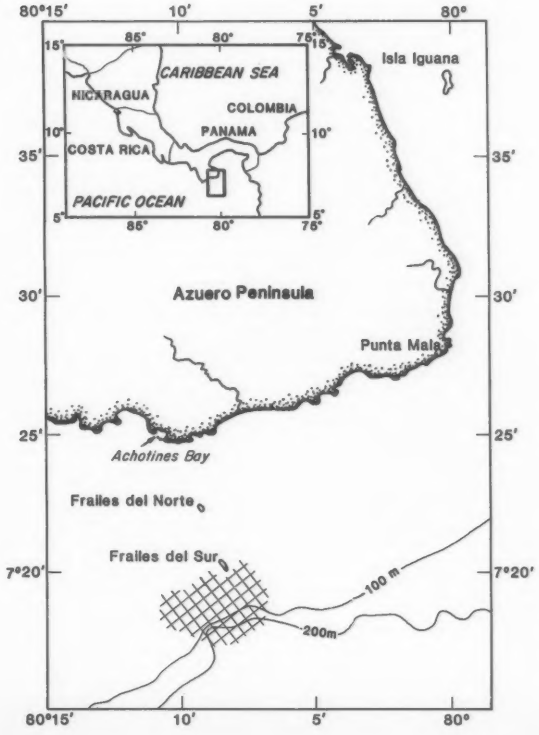

Figure 1
Location of the study site (cross-hatched) south of Achotines Bay, Panama. The IATTC's Achotines Laboratory is situated on the east side of the Bay.

Black skipjack tuna *Euthynnus lineatus* are not commercially important; however, their similarity to other tunas makes them valuable subjects of study. Their distribution is limited to tropical and subtropical regions of the eastern Pacific Ocean (Collette and Nauen 1983), with two stray specimens reported from the Hawaiian Islands (Matsumoto 1976). For many years, *E. lineatus* was thought to inhabit only coastal waters and waters around islands (Calkins and Klawe 1963, Yoshida 1979). However, recent fishing records show that black skipjack also occur in oceanic habitat (Schaefer 1987, fig. 1; Bayliff 1988a, fig. 62).

Clemens (1956) reported the only previous information on rearing and growth rates of early-juvenile black skipjack. Some information was reported by Peterson (1983:54) on the growth of 32–51 cm fork length (FL) black skipjack in the field, based on tagging studies and length-frequency modal progression analysis. Houde and Richards (1969) described the growth of larval little tunny *E. alletteratus* reared in the laboratory from planktonic eggs. The larvae were fed unspecified quantities of mostly copepod nauplii and copepodites, and grew from less than 3.0 mm total length at hatching to almost 8.5 mm in 18 days, a rate of about 0.3 mm/day. No data are available on larval growth of kawakawa *E. affinis* (Yoshida 1979).

The purpose of this note is to report the establishment of the Achotines Laboratory in Panama, to describe sampling results and rearing procedures of late-larval and early-juvenile black skipjack tuna, and to report growth experiments on captive black skipjack.

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Fishery Bulletin, U.S. 88:821–828.

Laboratory studies of growth are important in light of evidence in other fishes that variability in growth rates in the wild can affect early-life-stage duration, potentially resulting in large changes in larval survival and subsequent recruitment (Houde 1987).

The Achotines Laboratory and study area

The IATTC's Achotines Laboratory is located on a broad south-facing headland on the southern tip of the Azuero Peninsula in the Los Santos Province of the Republic of Panama (Fig. 1). This site is located at the northwestern part of the Panama Bight, which extends from Panama to Ecuador (Forsbergh 1969). The Panama Bight is a region with large seasonal variations in atmospheric and oceanic characteristics, in part influenced by the seasonal position of the intertropical convergence zone (ITCZ). Sea-surface temperature data (Fig. 2) clearly show an upwelling cycle driven by the Caribbean trade winds when the ITCZ is displaced to the south, typically beginning in December and lasting at least through April. The continental shelf is narrow, 2–30 km in width, off the Azuero Peninsula, but widens abruptly on either side of the Peninsula. Thus, oceanic habitat, thought to be a requirement for tuna spawning, occurs close to shore. Scombrid larvae and early juveniles are routinely captured as close as 9 km from Achotines Bay. The following late-larval and early-juvenile scombrids have been captured and held in the laboratory with varying degrees of success: black skipjack tuna, yellowfin and/or bigeye tuna (*Thunnus albacares* and/or *T. obesus*)[1], frigate and/or bullet tuna (*Auxis thazard* and/or *A. rochei*)[2], sierra *Scomberomorus sierra*, chub mackerel *Scomber japonicus*, and Indo-Pacific bonito *Sarda orientalis*.

Materials and methods

Larval and early-juvenile fishes were attracted to a bright underwater light at night (nightlighting) in the vicinity of the 100- and 200-m isobaths (Fig. 1) during October 1986–April 1988. A 24-volt DC 300-watt light was lowered from a drifting boat to a depth of about 14 m, left for about 5 minutes, and slowly raised to a depth of 1–2 m. Late-larval and early-juvenile[3] black skipjack tuna approaching the light were collected by dipnet and quickly placed into 61 × 76 cm polyethylene bags with rounded corners containing aerated seawater. A water conditioner, Fritz-guard, was added to the water to minimize damage to the fish from mucous loss caused by abrasion. Time from capture to arrival at the laboratory ranged between 1 and 3 hours. Sea-surface temperature, weather, and sea conditions were recorded. The fish which did not survive nightlighting and transfer procedures were measured (standard length, SL, to nearest 0.1 mm) and weighed (round wet weight to nearest 0.001 g) soon after capture.

At the laboratory, the captive fish were placed in 1.2-m diameter circular fiberglass tanks containing 0.3 m^3 of aerated seawater with a weak current. Water

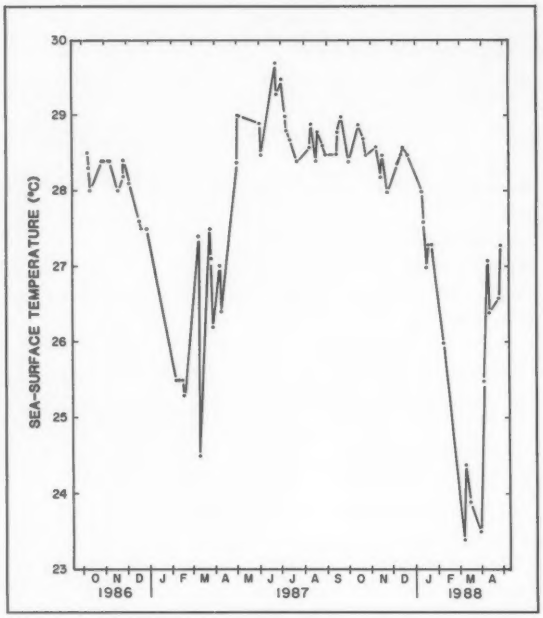

Figure 2
Sea-surface temperatures taken while nightlighting in the sampling areas (Fig. 1) off the Achotines Laboratory.

[1]Early-juvenile *T. albacares* and *T. obesus* cannot be distinguished on the basis of meristic, morphological, pigmentation (Matsumoto et al. 1972), or osteological characters (Potthoff 1974). However, an electrophoretic distinction between yellowfin and bigeye adults provides a means of separating the larvae and early juveniles (Graves et al. 1988).

[2]Larval and early-juvenile *Auxis thazard* and *A. rochei* have been distinguished by minor differences in pigmentation and body depth, but identifications are ambiguous (Uchida 1981). Gill raker counts can be used for identification of juveniles >25 mmSL, but gill rakers are too tiny and difficult to count in smaller specimens (Uchida 1981).

[3]Late larvae are defined as the "postflexion larvae" and "transformation larvae," and early juveniles as the "pelagic or special juveniles" of Kendall et al. (1984).

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

from Achotines Bay was pumped through a sand filter containing #20 silica sand and added to the tanks at a rate sufficient to exchange the water several times per day. Wild zooplankton, predominantly copepods, caught with a 505-μm mesh net were provided as food in densities of approximately 50–150/L two or three times per day until the black skipjack grew to about 13–17 mmSL. Then, whole *Poecilia latipinna* and *Poeciliopsis turrubarensis* fry or chopped fish of several species were provided four to six times per day. The black skipjack were fed until satiated. Maximum rations were provided throughout the growth experiments. When the fish reached about 35–45 mmSL, they were transferred into 3.0-, 4.6-, or 6.4-m diameter plastic-lined pools containing 2.3, 11.4, or 24.6 m^3 of water.

Water temperature in the laboratory aquaria was recorded to the nearest 0.1°C several times per day with a mercury thermometer. Salinity was measured to the nearest 1‰ (readability) several times per month with an optical salinometer. Daylight illumination was supplemented by fluorescent lights over the containers. At night, low levels of indirect fluorescent lighting were maintained to prevent the fish from colliding with the container walls.

Because black skipjack are delicate, initial lengths of those held for growth experiments were estimated by visually comparing them with a ruler held near the tank and adjusting for the magnifying effect of the water. Lengths of fish that had recently died or were near death in the tanks soon after capture were estimated in the same way, and subsequently measured (SL to nearest mm) after retrieval from the tanks to improve estimating skills and to provide a measure of estimation error. The maximum error measured was used to calculate the largest potential errors in growth rates that could have resulted.

Weights were calculated from lengths based on a weight-length relationship derived from 184 black skipjack measured (SL to nearest 0.1 mm) and weighed (round wet weight to nearest 0.001 g) soon after capture. Length and weight measurements were converted to natural logarithms (ln), and regression parameters ln$a$ and b were estimated by the method of least squares,

$$\ln W = \ln a + b \ln SL, \quad (1)$$

where W = weight in g, and SL = standard length in mm. Validity of the assumptions of linear regression were tested using residual analyses (Draper and Smith 1981).

Standard lengths and weights at the end of the growth experiments were measured to the nearest 0.1 mm and 0.1 g, respectively. The experiments were terminated when the fish died from some accidental or unknown cause or were near death.

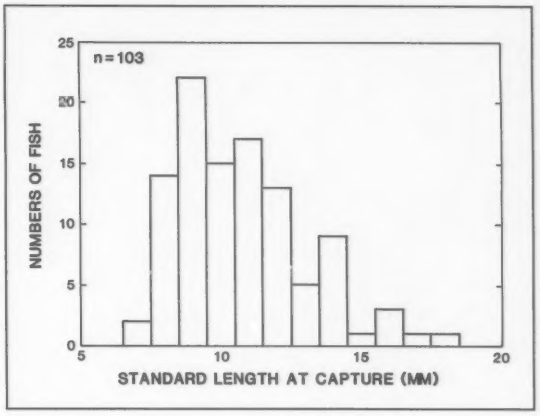

Figure 3
Standard lengths of late-larval and early-juvenile black skipjack tuna measured soon after capture by nightlighting in the waters south of the Achotines Laboratory, October 1987–April 1988.

The average daily growth rate of each fish over the duration of captivity was expressed as growth in SL (mm) during captivity divided by days in captivity. The average daily weight increase of each fish was calculated using final weights of the fish and the estimated SL at capture converted to weight.

Results

Late-larval and early-juvenile scombrids have been captured in all months of the year, but not in every month since the inception of routine sampling in 1984. During the period of October 1986–April 1988, 212 late-larval or early-juvenile black skipjack tuna were captured and transferred to the laboratory. Specimens which did not survive live transfer procedures ranged between 7.1 and 18.4 mmSL soon after capture (Fig. 3). A total of 79 (37%) survived handling and lived longer than 48 hours. Sampling dates, numbers caught, and other information are given in Table 1. Young black skipjack were caught during 16 of the 18 months in which sampling took place during this period. No nightlighting took place during January 1987 due to poor weather conditions. The greatest catches were made during November and December 1986, December 1987, and January 1988. Sampling frequency was governed by weather conditions, boat availability, and other factors. At times, sampling was terminated prematurely due to poor weather, which resulted in no catch. For this and other reasons, the

Table 1

Sampling information, numbers of late-larval and/or early-juvenile black skipjack which survived at least 48 hours after transfer to laboratory aquaria, and standard lengths of those which did not survive nightlighting and transfer procedures. Accurate measurements were not obtained from all those which did not survive.

Date	Sea-surface temp. (°C)	No. caught	Standard length at capture: Mean	Range	SD	*n*	No. surviving
1986							
8 Oct.	28.5	7	15.8	13.6–17.0	1.279	5	2
9 Oct.	28.3	0	—	—	—	—	—
11 Oct.	28.0	0	—	—	—	—	—
28 Oct.	28.4	17	11.4	9.4–15.3	1.631	16	1
29 Oct.	28.4	10	11.8	10.2–12.8	1.124	5	5
31 Oct.	28.4	0	—	—	—	—	—
5 Nov.	28.4	0	—	—	—	—	—
8 Nov.	28.4	0	—	—	—	—	—
19 Nov.	28.0	11	9.3	7.7–11.1	1.047	8	2
20 Nov.	28.0	2	—	—	—	—	1
26 Nov.	28.2	9	—	—	—	—	4
27 Nov.	28.4	4	—	—	—	—	0
4 Dec.	28.1	3	11.5	9.4–13.2	1.930	3	0
18 Dec.	27.6	2	10.5	10.0–11.0	0.707	2	0
22 Dec.	27.5	1	—	—	—	—	0
29 Dec.	27.5	0	—	—	—	—	—
1987							
6 Feb.	25.5	0	—	—	—	—	—
16 Feb.	25.5	0	—	—	—	—	—
17 Feb.	25.3	4	9.8	7.7–11.9	2.970	2	2
18 Feb.	—	0	—	—	—	—	—
9 Mar.	27.4	0	—	—	—	—	—
12 Mar.	24.5	0	—	—	—	—	—
25 Mar.	27.5	2	11.9	—	—	1	1
26 Mar.	27.1	0	—	—	—	—	—
30 Mar.	26.2	0	—	—	—	—	—
3 Apr.	—	0	—	—	—	—	—
8 Apr.	27.0	0	—	—	—	—	—
9 Apr.	26.4	0	—	—	—	—	—
1 May	28.4	0	—	—	—	—	—
4 May	29.0	2	9.4	—	—	1	1
6 May	29.0	0	—	—	—	—	—
1 June	28.9	0	—	—	—	—	—
3 June	28.5	0	—	—	—	—	—
4 June	28.5	0	—	—	—	—	—
25 June	29.7	0	—	—	—	—	—
26 June	29.3	0	—	—	—	—	—
2 July	29.5	0	—	—	—	—	—
7 July	29.0	3	12.0	—	—	1	2
9 July	28.8	0	—	—	—	—	—
1987 (continued)							
14 July	28.7	3	—	—	—	—	2
23 July	28.4	5	12.8	11.5–14.0	1.770	2	0
10 Aug.	28.6	0	—	—	—	—	—
11 Aug.	28.9	0	—	—	—	—	—
18 Aug.	28.4	0	—	—	—	—	—
20 Aug.	28.8	4	—	—	—	—	4
27 Aug.	28.6	0	—	—	—	—	—
31 Aug.	28.5	0	—	—	—	—	—
15 Sep.	28.5	3	10.5	—	—	1	2
17 Sep.	28.8	3	16.4	14.4–18.4	2.830	2	1
23 Sep.	29.0	6	8.1	—	—	1	1
2 Oct.	28.4	7	12.7	11.2–13.7	1.162	4	3
15 Oct.	28.9	0	—	—	—	—	—
23 Oct.	28.7	1	—	—	—	—	1
26 Oct.	28.5	1	—	—	—	—	0
9 Nov.	28.6	4	11.5	10.0–13.7	1.565	4	0
16 Nov.	28.2	3	—	—	—	—	3
17 Nov.	28.5	1	—	—	—	—	1
23 Nov.	28.0	0	—	—	—	—	—
9 Dec.	28.4	37	8.6	7.1–9.5	0.728	24	5
15 Dec.	28.5	8	10.3	9.5–11.7	1.217	3	5
16 Dec.	28.6	4	—	—	—	—	4
22 Dec.	28.5	4	8.0	7.9–8.0	0.071	2	2
1988							
1 Jan.	28.0	0	—	—	—	—	—
13 Jan.	27.6	0	—	—	—	—	—
18 Jan.	27.0	0	—	—	—	—	—
20 Jan.	27.3	36	11.3	9.0–14.4	1.717	13	23
25 Jan.	27.3	0	—	—	—	—	—
10 Feb.	26.0	1	12.2	—	—	1	0
8 Mar.	23.4	0	—	—	—	—	—
10 Mar.	24.4	2	10.9	—	—	1	1
16 Mar.	23.9	0	—	—	—	—	—
30 Mar.	23.5	0	—	—	—	—	—
5 Apr.	25.5	0	—	—	—	—	—
11 Apr.	27.1	1	9.2	—	—	1	0
13 Apr.	26.4	1	—	—	—	—	0
26 Apr.	26.6	0	—	—	—	—	—
28 Apr.	27.3	0	—	—	—	—	—
Total		212				103	79

capture frequency of black skipjack in Table 1 is not meant to reflect the true spawning frequency of the adults.

Thirty-nine specimens were held for laboratory growth experiments. Their estimated lengths and weights at capture are shown in Figure 4. The larger fish in the catch (Fig. 3) survived capture and transfer in greater proportions than the smaller ones (Fig. 4). The captive fish survived an average of 36 days in the laboratory; most (64%) died in 30 days or less. Three fish survived in excess of 130 days. The longest-lived black skipjack grew in captivity for 167 days, and attained an SL of 259 mm and weight of 336 g. It was sacrificed when it ceased feeding due to eye infec-

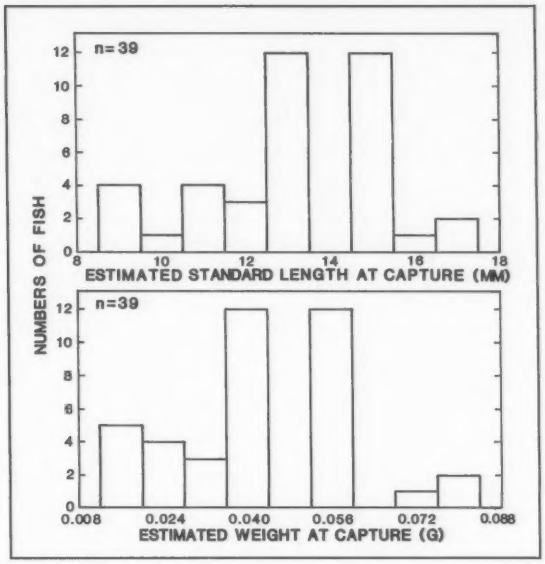

Figure 4

Standard lengths estimated in the laboratory and weights calculated from a weight-length regression (Fig. 6) for 39 black skipjack tuna held for growth experiments.

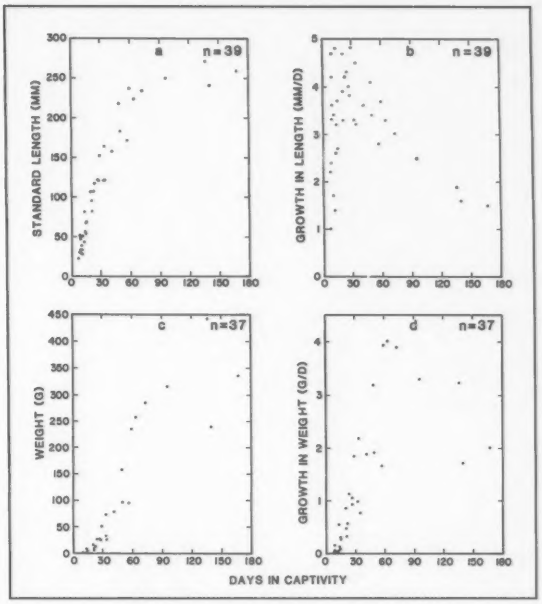

Figure 5

Standard lengths (a), growth rates in standard length averaged over the duration of captivity (b), weights (c), and growth rates in weight averaged over the duration of captivity (d) of juvenile black skipjack tuna at the end of laboratory growth experiments versus days in captivity. Two fish held 11 days were not weighed.

tions. Water temperature and salinity in the laboratory aquaria ranged from 23.7 to 29.1°C and 29 to 34‰, respectively, over all the experiments.

Growth in length

Captive black skipjack fed *ad libitum* grew in a curvilinear relationship of SL with time (Fig. 5a). The data were not fitted to derive a predictive growth equation because they are inadequate for that purpose. The fish were fed to satiation, but the rations were not measured.

The highest rates of growth in length were attained during the first month in captivity (Fig. 5b). After about 4 weeks, the fish had progressively lower average growth rates. Black skipjack from experiments that terminated during the first 15 days of captivity grew at extremely variable rates, from 1.0 to 4.8 mm/day. After 15 days, there was a significant negative correlation between growth rate and days in captivity ($r = -0.877$, $n = 23$, $P \ll 0.001$). All the fish that survived between 15 and 50 days grew rapidly, 3.2–4.8 mm/day. After about 50 days in captivity average growth rates declined drastically.

Errors in estimating lengths of newly-captured fish that had recently died or were near death in the tanks soon after capture ranged up to ±4 mm, although most were less. Maximum potential errors in growth rates were calculated based on the assumption that ±4-mm errors were made when estimating capture lengths of all the experimental fish. In general, the importance of measurement error diminished with increasing time in captivity. Potential errors ranged from only ±0.8 to a high of ±53.3% for one fish held the least time of all experimental fish (7.5 days). The next greatest error estimates were −26.1 and +23.8%, and the means were ±8.8%. Potential errors for the majority (85%) of the samples were ±13.5% or less, and less than 10% for all fish held in captivity more than 15 days ($n = 25$).

Growth in weight

Growth in weight appeared to follow a sigmoidal relationship with time in captivity (Fig. 5c). The rate of weight gain during the first 30 days was low, increasing dramatically between about 30 and 70 days, and then tapering off after 70 days.

While the greatest and most variable growth rates in length took place during the first 30 days, average rates of weight gain during that period were less than

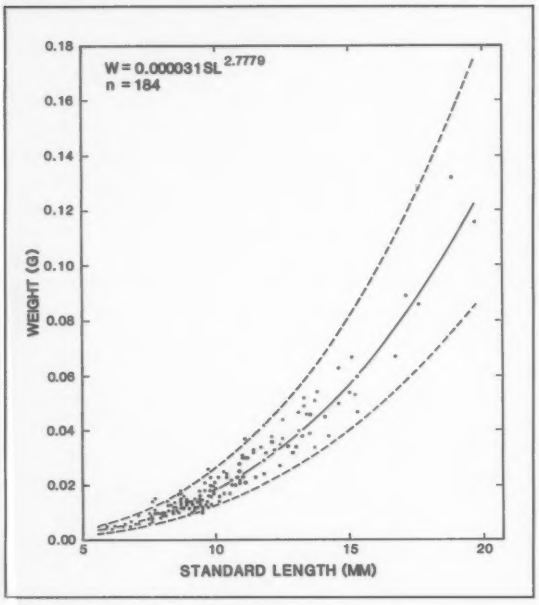

Figure 6

Weights (W) and standard lengths (SL) of 184 late-larval and early-juvenile black skipjack tuna measured soon after capture. The power function of the log-log fitted regression line and 95% prediction belts of weight on length are included. The r^2 of the log-log fit was 0.927, the 95% confidence limits of the regression coefficient were 2.6641–2.8917 g/mm, and the standard error of the estimate was 0.1790.

those for fish held longer (Fig. 5d). The greatest average growth rates in weight (3.9–4.0 g/day) were recorded for fish surviving 60–73 days ($n = 3$). After that time, average daily weight increases declined drastically ($n = 4$).

Weight-length relationship

Capture weights of the live black skipjack held for growth experiments (Fig. 4) were estimated using a weight-length regression equation based on fresh measurements and weights of 184 other black skipjack ranging from 5.6 to 19.7 mmSL and 0.004 to 0.132 g (Fig. 6). The power function of the fitted regression is $\ln W = -10.3806 + 2.7779 \ln SL$. The standard errors of parameters $\ln a$ and b are 0.1326 and 0.0577, respectively.

Tests for normality of the residuals (Filliben 1975), independence or lack of autocorrelation of the residuals (Durbin-Watson statistic), and a constant variance (homoscedasticity) of the residuals (Wesolowski 1976) failed to indicate any violation of the assumptions of linear regression.

Effect of temperature

Sea-surface temperatures during each sampling trip are shown in Figure 2. The data show a gradual decline in temperatures commencing in November or December, reaching lows of about 23–25°C in March, followed by a gradual warming to maximum stable temperatures of about 28–29°C from April or May until October or November. Black skipjack spanning the entire size range encountered (7.1–18.4 mmSL) were taken when the temperature ranged between 28.0 and 29.0°C. Only smaller individuals (7.7–12.2 mmSL) were caught when sea-surface temperatures were below 27.0°C, but the sample size was low ($n = 4$).

Neither the growth rates nor final sizes attained in captivity were significantly correlated with mean water temperatures in the aquaria over the course of the experiments. However, the final lengths ($r = -0.559$, $P<0.001$) and weights attained ($r = -0.572$, $P<0.001$), average daily growth in weight ($r = -0.503$, $0.001< P<0.002$), and the number of days in captivity ($r = -0.568$, $P<0.001$) were negatively correlated with minimum temperatures recorded in the laboratory. No such relationships were observed with the maximum temperatures recorded.

Discussion

Except for the black skipjack held in shipboard aquaria by Clemens (1956), these experiments are the first in which late-larval or early-juvenile tunas were collected in the wild and reared in captivity for experimental growth studies. Similar experiments on other scombrids are being conducted at the Achotines Laboratory. To our knowledge, 167 days is the longest time any scombrid has been held in captivity beginning at an early life stage. Harada et al. (1973) held *Auxis tapeinosoma* (= *A. rochei*) larvae for 52 days, Harada et al. (1974) reared *Sarda orientalis* larvae up to 99 days, and Harada et al. (1980) grew *Thunnus albacares* larvae for a maximum of 38 days. These larvae were all hatched from artificially-fertilized eggs obtained from ripe females, and fed unspecified rations of zooplankton and fish larvae. Previous to our studies, young *E. lineatus* were reared on only one occasion. Clemens (1956) collected black skipjack by dipnet at night, and held 10 individuals averaging about 27 mmSL for up to 12 days in shipboard aquaria. Average growth in length was 3.1–3.6 mm/day. The paper does not state at what water temperature the fish were held nor how much food was provided during the experiment. The growth rates measured in Harada et al.'s (1973, 1974, 1980) experiments were 3.0, 3.0, and 1.3 mm/days, respectively. The growth rates reported by Clemens

(1956) and Harada et al. (1973, 1974, 1980) are within the range of growth rates reported here, although we obtained greater rates too, up to 4.8 mm/day. Clemens (1956) stated that his results probably approximate minimum growth rates in nature.

An undesirable aspect of our study was the necessity of estimating, rather than measuring, lengths at the time of capture. This may have contributed to the large variance in the data reported for the first 15 days (Fig. 5b). Estimation errors were minimal, however, because the second author's ability to estimate lengths of live fish was continually refined by estimating, then measuring the fish that died in the tanks soon after capture. Except for a few fish held for short times, maximum estimation errors of ±4 mm translated to low potential error in growth rates.

Despite unavoidable estimation errors, this study reveals some interesting aspects of growth of young tunas. Black skipjack are capable of growing at high but variable rates when food is plentiful. The growth rates we measured might be considered upper limits for this species; feeding to satiation in the wild would likely be detrimental to survival because laboratory observations suggest that the added weight of food in the gut inhibits mobility. The variability in rates measured during the early part of the experiments may be due in part to the stress of captivity. However, high, variable growth rates suggest a large scope for growth (Brett 1979), an advantageous characteristic for fish that spend their early life stages in the epipelagic zone where predation risk is great. A large scope for growth permits rapid growth when food is abundant, providing young tunas an earlier transition to piscivorous feeding and early formation of schools. The decline in growth rates with increasing time in captivity may be related in part to inadequate-sized rearing containers (Theilacker 1980). Further laboratory growth experiments should concentrate on maintaining constant, controlled rations.

Growth rates of late juvenile and/or adult black skipjack from the commercial catch in the eastern Pacific Ocean are much lower, as expected, than those reported here. Tagging and length-frequency modal progression analyses provided rates that agree with each other (Peterson 1983:54–55). Black skipjack measuring 32–45 cmFL grew about 0.36 mm/day. Larger fish, 45–51 cm, grew more slowly, 0.22 mm/day. The upper seven data points in Figure 5a, corresponding to the largest fish (224–272 mmSL) which were held for the longest times (59.5–167.5 days), appear to represent a slower growth stanza than a previous stanza <60 days. A straight line fitted to these seven points yielded a significant slope of 0.28 mm/day, comparable to the natural growth rates reported for 32- to 51-cm black skipjack (Peterson 1983:54–55). Skipjack tuna *Katsuwonus pelamis*, another primitive species of the tribe Thunnini, measuring 37.5–42.5 cmFL when tagged and released east of 100°W longitude grew an average of 1.22 mm/day in 31–180 days at liberty (Bayliff 1988b).

Much additional work on growth of tunas under controlled conditions, as well as growth studies in nature, is needed to understand how physical and biotic variability in the ocean affects growth rates and life-stage duration. By virtue of black skipjack's biological similarities to commercially important tunas, we believe that such studies utilizing black skipjack tuna will yield important information that would be applicable to other tunas.

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We wish to thank the staff members of the Achotines Laboratory for their hard work and long hours. R.R. Lauth and R.C. Jope provided special assistance with weight-length and laboratory temperature data. We acknowledge the efforts of G. Schumann, B.M. Chatwin, and J.M. Ianelli for much of the early development of the Achotines Laboratory. The Panamanian Ministerio de Comercio e Industria, Departamento de Recursos Marinos, has provided continued support of the Achotines Laboratory. Valuable reviews were provided by W.H. Bayliff, W.L. Klawe, R.R. Lauth, D. Margulies, K.M. Schaefer, and two anonymous reviewers.

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Length-weight, Age and Growth, and Landings Observations for Sheepshead *Archosargus probatocephalus* from North Carolina

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Sheepshead *Archosargus probatocephalus* range from Nova Scotia to Brazil (Robins and Ray 1986). Three subspecies have been recognized, based on the number and size of body bars: *A. p. probatocephalus* ranges along the Atlantic coast of the United States; *A. p. oviceps*, from St. Mark's, Florida tc the Campeche Banks; and *A. p. aries*, from Belize to Babia de Sepetiba, Brazil (Caldwell 1958, 1965). Little is known concerning length-weight or age and growth relationships for this common edible fish.

This paper presents the age and growth and length-weight relationships, reviews changes in historical catch for sheepshead from North Carolina, and resolves discrepancies in the literature concerning maximum length and weight of this species (Hildebrand and Schroeder 1928, Hildebrand and Cable 1938, Bigelow and Schroeder 1953, Robins and Ray 1986).

Methods

Most specimens were captured in 12-m otter trawls, 91-m gillnets, or by spear. Most specimens were obtained from two sites where sheepshead are presently common in North Carolina: the Masonboro and Carolina Beach Inlets-Cape Fear River area of New Hanover and Brunswick counties, and Radio Island Jetty, Carteret County, extending from Beaufort Inlet in the Atlantic Ocean to just south of Shackleford Banks and Cape Lookout Jetty. The largest specimens and the state record-sized fish were caught in the Carolina Beach area by hook-and-line fishermen as part of the state's fishing citation program. Specimens were measured to the nearest millimeter standard (SL) and total length (TL) and weighed to the nearest gram, except for the tournament fish, which represented the upper end of the length-weight curve and were weighed to the nearest 114 g. Conversion from total length to standard length, for study fish larger than 100 mmSL, was possible by the formula $SL = 0.817TL$, $N = 240$; for fish smaller than 100 mmSL the conversion formula was $SL = 0.780$ TL. The latter conversion was determined by utilizing data for 412 young specimens (6–48 mm) measured by Hildebrand at Beaufort, North Carolina in 1914 (Hildebrand's field notes, Inst. Mar. Sci., Morehead City). Length-weight and standard length-scale radius relationships were calculated using log-log formulas where $\log(y) = a + b \log(x)$, where x is either standard length or scale radius, measured from the focus to the outer lateral edge of the scale, and y equals weight.

Scales were removed for ageing from just below the spinous/soft-ray dorsal-fin junction and the area above the lateral line. Scales were read at 10K magnification using a Baush and Lomb dissecting microscope. No validation of annulus formation was attempted considering the diverse availability of specimens. Therefore, the values I report are only presumed ages.

Results

The length-weight relationship for 282 sheepshead, measuring 9–591 mmSL (723 mmTL) and weighing 0.042–8370 g (18 lb, 7 oz), was calculated by the formula $\log(y) = -4.5287 + 3.0446 \log(x)$, $r = 0.9929$ (Fig. 1).

A linear relationship between standard length and scale radius was described for 68 fish measuring 31–525 mmSL by the formula $\log(y) = 0.8801 + 0.820 \log(x)$, $r = 0.9789$. Too few scales from specimens smaller than 30 mm were available for inclusion in the relationship calculation. Scales of fish 17–400 mmSL or those to age 4 were easy to read. Scales of older and larger specimens were difficult to read as the focus often became opaque and thickened, thereby obscuring the first two annuli.

Backcalculations of age and size from 50 of the best scales suggested seven age-classes (Table 1); however, these did not agree with a simple length-frequency plot where eight age classes seemed to prevail (Fig. 2). Also the maximum backcalculated size was 482 mm, whereas the largest fish studied was 525 mmSL. This discrepancy strengthened the observation that perhaps one or two annulae were obscured on scales of specimens larger than 400 mmSL, which were probably older than 8 years of age.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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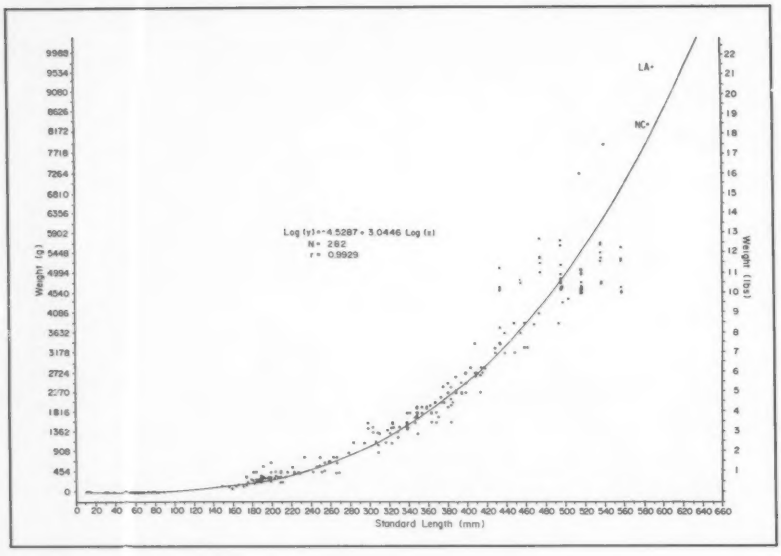

Figure 1
Length-weight relationship for 282 sheepshead captured in North Carolina. NC = largest North Carolina specimen; LA = world record Louisiana sheepshead.

Table 1
Backcalculation of standard lengths at presumed age for sheepshead from North Carolina.

		Age							
N	Y of Y	1	2	3	4	5	6	7	8
2	67	91							
30	73	156	189						
1	74	142	218	237					
1	106	158	205	248	295				
7	100	177	242	316	349	381			
7	81	135	242	274	325	366	387		
1	95	140	225	322	351	372	411	432	
1	97	138	222	266	355	397	422	466	482
		Weighted mean							
50	79	152	207	289	336	375	394	449	482
		Increment							
		73	55	82	47	39	19	55	33

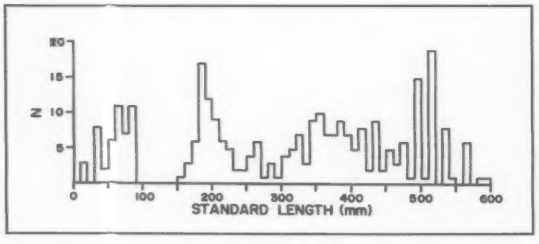

Figure 2
Length-frequency histogram, in 10-mm units, of the 282 sheepshead captured in North Carolina.

Discussion

Only Ogburn (1984) has examined the length-weight of sheepshead from Masonboro Inlet Jetty, New Hanover County, NC. Her specimens measured 56–340 mmSL and weighed 4.3–1535 g, $N = 45$; data on five extremely small specimens, 56–63 mmSL, were excluded from the length-weight relationship. However, recalculation of this relationship, using all data, yielded the equation $\log (y) = -4.6927 + 3.1309 \log (x)$, $r = 0.9829$. Superimposing that recalculation on Figure 1 indicated good agreement between her data and that reported here.

Mook (1977) noted scales on 10–12 mm specimens. Johnson (1978) noted no scales for specimens of 12-mm lengths, but did depict them on a 17-mm specimen. North Carolina specimens smaller than 16 mm possessed no scales but their outlines were present on 11–12 mmSL specimens.

A variety of structures have been used to age fishes (Summerfelt and Hall 1987). The reason only scales were used to age sheepshead was that they were the only structures consistently available during this study, as the fish were obtained from many sources or could not be kept for age determination by vertebra, otoliths, etc.

The largest sheepshead from nearby South Carolina were 513 mmSL (641.4 mmTL) weighing 6015.5 g, and 505 mmSL (625 mmTL) weighing 4900 g (D. Hammond and E. Wenner, S.C. Wildl. Mar. Res. Dep., Charleston, pers. commun., Jan. 1990). These data also fall within the length-weight curve plotted for North Carolina sheepshead (Fig. 1).

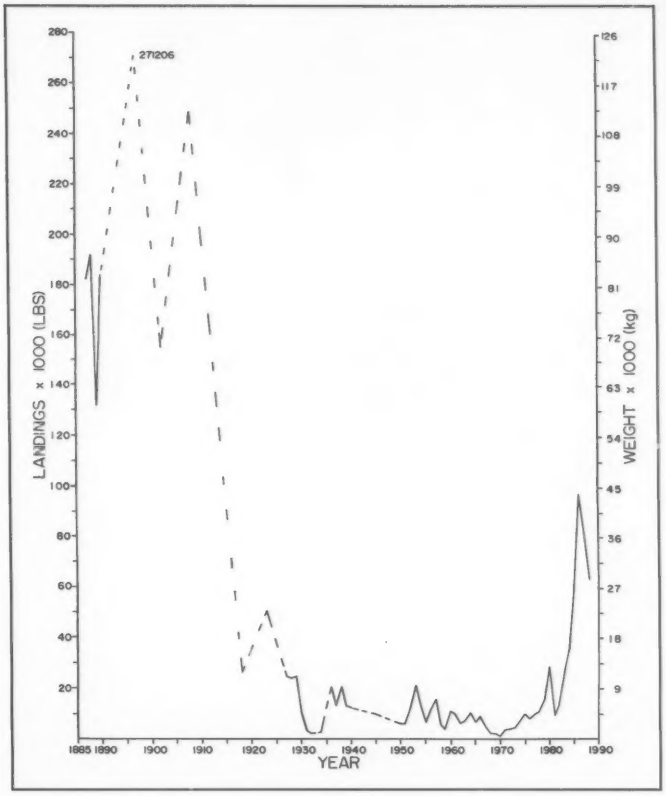

Figure 3
North Carolina catch landings for sheepshead, 1887–1989. Dashed lines indicate missing year data.

Like Hildebrand and Cable (1938) for Beaufort, NC, and Springer and Woodburn (1960) for Gulf of Mexico sheepshead, the smallest North Carolina sheepshead were also captured between May and October. Note the peculiar hiatus in the length frequency and length-weight curve (Figs. 1, 2) for sheepshead 90–150 mmSL. Absence of specimens within these size ranges may have been caused by their shifting from a seagrass habitat to piling, jetty, and other hard substrates preferred by larger young and adults (Hildebrand and Cable 1938, Johnson 1978).

A search of major museums and taxidermist records has failed to uncover sheepshead that attain the size and weight (91 cm and 9–13.5 kg) reported in the literature (Hildebrand and Schroeder 1928, Hildebrand and Cable 1938, Bigelow and Schroeder 1953, Robins and Ray 1986). Even if 91 cm was an accurate total-length measurement, conversion to SL would make that specimen 743 mm, a size far larger than even the officially recognized world-record specimen from Louisiana (probably *A. p. oviceps*), which was 596 mmSL and 730 mmTL, and weighed 9648 g (21 lb, 4 oz, and plotted in Figure 1) and would fall far outside the length-weight data depicted in Fig. 1. This is strong evidence that sheepshead do not attain the large sizes mentioned in the literature. In essence, future literature should be emended to note that the maximum sizes of sheepshead in North Carolina, to date, are 591 mmSL, 723 mmTL, weighing 8370 g, and elsewhere 596 mmSL, 730 mmTL, weighing 9248 g. All larger sizes reported should remain or be considered erroneous.

A dramatic shift in the commercial landings of sheepshead (mostly caught by haul seine) has occurred in North Carolina between 1887 and 1989 (Fig. 3) (Chestnut and Davis 1975; Goode 1884; NC Div. Mar. Fish. statistical data, Morehead City). Yarrow noted (Smith 1907) that sheepshead were very abundant in 1871. Commercial catches prior to 1900 remained over 61500 kg. Catches between 1918 and 1981 remained low (27000–47000 kg, lowest in 1970, 675 kg). Only since 1981 has a recent surge been noted in the landings (Fig. 3), mostly in Carteret County.

Hildebrand and Cable (1938) and Johnson (1978) noted that larval and juvenile sheepshead are usually found associated with seagrasses which they depend

upon for shelter and food. Whether the early and recent landings can be correlated with seagrass abundance remains unknown, for no early records of seagrass abundance exist prior to and following the wasting disease of the 1930s (Orth and Moore 1981, Short et al. 1987). To date, the beds have seemingly not increased (G. Thayer, NMFS Beaufort Lab., pers. commun., Jan. 1990). It would have been beneficial to know whether the early-life-history stages that depend on vegetation for food and protection were or are increasing in relation to seagrass incidence and just how dependent they are on that habitat for their growth and survival.

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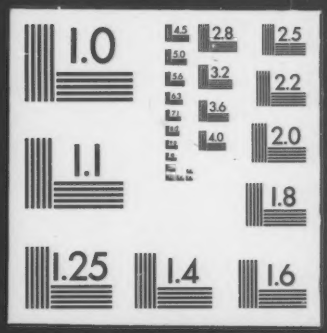
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